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The Photosynthetic Pigments of Lake Superior Periphyton and Their Relation to Primary Productivity

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FOREWORD

This Bulletin is published in furtherance of the purposes of the Water Resources Research Act of 1964. The purpose of the Act is to stimulate, sponsor, provide for, and supplement present programs for the conduct of research, investigations, experiments, and the training of scientists in the field of water and resources which affect water. The Act is promoting a more adequate national program of water resources research by furnishing financial assistance to non-federal research.

The Act provides for establishment of Water Resources Research Institutes or Centers at Universities throughout the Nation. On Sept. 1, 1964, a Water Resources Research Center was established in the Graduate School as an interdisciplinary component of the University of Minnesota. The Center has the responsibility for unifying and stimulating University water resources research through the administration of funds covered in the Act and made available by other sources; coordinating University research with water resources programs of local, State and Federal agencies and private organizations throughout the State; and assisting in training additional scientists for work in the field of water resources through research.

This report is number 18 in a series of publications designed to present information bearing on water resources research in Minnesota and the results of some of the research sponsored by the Center. The study with which this report is concerned was designed to measure productivity and explore the biodynamics of Lake Superior periphyton. The biomass, community structure, and photosynthetic activity of epilithic periphyton from a representative area, Stony Point Bay, were determined by examination of a variety of parameters. Naturally occurring periphyton and regrowth organisms were studied. In addition, the attached communities of other north shore stations were examined and data reflecting the effects of certain environmental conditions on the productivity of periphyton were acquired.

It is believed that the data collected will provide a baseline for detecting the gradual advance of eutrophication in Lake Superior. Additional studies are being supported by the Center.

INTRODUCTION

Primary production by algal communities may be measured by either of two general methods, each with its own special applicability. One is the evaluation of the "standing crop", or the determination of biomass, which is quite significant when attention is paid to the rate of establishment and "turnover" of the communities. The other method involves the investigation of the dynamics of energy transfer through the communities, or more specifically, the determination of photosynthetic rates. The estimation of "standing crop" may include taxonomic studies, the determination of numbers of organisms, the measurement of weight or volume of the communities, or the quantitative analysis of some component of the organisms, such as carbon, nitrogen, photosynthetic pigments, or DNA. The measurement of photosynthetic and respiratory rates may be used to calculate gross primary productivity (the total rate of photosynthesis including the organic matter used up in respiration) and net primary productivity (the rate of storage of organic matter in plant tissues in excess of respiratory utilization). The latter may also be termed "apparent photosynthesis" or "net assimilation." When both "standing crop" and assimilation rates for all communities of primary producers have been determined, the true basic productivity of an ecosystem may be calculated.

Algae are found virtually everywhere in the lentic environment where light intensity is sufficient to support their growth. Specific types of algae, however, occupy different habitats within the boundaries of a lake, and separate descriptive terms are applied to those communities found in each distinct habitat. Plankton are those microscopic or near-microscopic organisms which are non-motile or weakly motile and whose movements are more or less dependent on currents. Animal forms, such as crustaceans and rotifers, are called zooplankton, and algal forms are termed phytoplankton. Members of the phytoplankton are usually the major primary producers in a large, deep lake, but other algal communities contribute to the production to a certain, and often unknown, degree. When algae are associated with the water surface film, they constitute part of the neuston. Those living in beach sand are called psammon. Algae which become entangled with attached forms, but are not themselves attached to a substrate, are known as merophyton. Truly attached forms of algae which break loose from a substrate and float free among the true plankton are referred to as tychoplankton.

Terminology referring to organisms which are attached to submerged substrata in water has been the subject of some controversy and is not entirely clear at this time. Much of the European literature is dominated by the German term "Aufwuchs", which is used broadly to include the entire sessile benthic community. Ruttner (1953) defines "Aufwuchs" as "those organisms that are firmly attached to a substrate but do not penetrate into it." Frey and Fry, the translators of Ruttner's text, suggest that such a connotation may include many organisms commonly grouped among the benthos. Despite this seeming disparity, "Aufwuchs" has been variously retained in community considerations (Odum _et al_., 1959; Reid, 1961), but occasionally in a more restricted sense (Odum, 1957). According to Wetzel (1964), Hentschel used "Bewuchs" in referring to attached organisms on glass plates, and this distinction was retained for a time in the works of some investigators, leaving "Aufwuchs" to describe colonization on submerged macroflora.

The term "periphyton" has been widely used in American literature, but has often been restricted to the attached communities of larger macrophytes or other living surfaces (Welch, 1952). Wetzel (1964) refers to an earlier definition by Roll, in which "periphyton" includes all sessile organisms on any type of substrate, divisible into two groups: (1) "lasion" (=Bewuchs), in which the organisms are thoroughly associated with one another in the phyto-sociological sense, and (2) "epiphyton" (=Aufwuchs), in which the organisms are not associated in this sense. However, Young (1945) defined periphyton more broadly and in a more descriptive manner as follows:

> "By periphyton is meant that assemblage of organisms growing upon free surfaces of submerged objects in water, and covering them with a slimy coat. It is that slippery brown or green layer usually found adhering to the surfaces of water plants, wood, stones, or certain other objects immersed in water and may gradually develop from a few tiny gelatinous plants to culminate in a wooly, felted coat that may be slippery, or crusty with contained marl or sand."

Some investigators, in an effort to avoid interpretation of the foregoing terms, have referred to the same community as "benthic algae" (Blum, 1956; Round, 1964), "benthos" (Lund and Talling, 1957), or "attachment materials" (Newcombe, 1949), but the use of these terms has not served to clear up the situation. While Young's broad delineation of periphyton must obviously include those organisms referred to by some as merophyton, his definition has been adopted for the purposes of this report. Although periphyton, defined in this manner, includes both plants and animals, it is known that this community is composed mostly of plant material which is mainly algal in nature; where the current investigation is concerned with enumeration of organisms, only the algae are counted. The further restricting term "epilithic periphyton" is used in this bulletin, since the organisms under investigation were growing upon rocks.

RELEVANT RESEARCH

European literature reveals more attention paid to the periphyton habitat in those countries than in the United States (Sladeckova, 1962); however, these studies are often of a limited type, contributing little to an understanding of the magnitude of periphyton productivity. Although the periphyton community has been recognized by many researchers as a significant part of the aquatic ecosystem, few systematic studies regarding its role or relative importance in primary production have been attempted. Prescott (1956) states that while the periphyton community should be of obvious concern to the ecologist and the limnologist, the habitat and life history of the attached algae have been largely ignored. This point is further emphasized in a lengthy review of the work relating to periphyton written by Alena Sladeckova (1962) in which she notes that attention paid the attached communities is extremely slight when compared with the numerous investigations of the plankton. The general neglect of freshwater periphyton communities continues in the United States even though enough production measurements of all components of the marine environment have been made to suggest that in many shallow areas the attached populations make major contributions to the primary productivity of embayments (Pomeroy, 1961). Evidently it is not unusual for production of benthic populations to exceed that of phytoplankton on a unit area basis in shallow waters. There is little doubt that some periphyton populations are more efficient than are phytoplankton in the utilization of available light.

The exclusive goal of a few investigations has been to determine the taxonomic character of certain periphyton communities. Most studies of the periphyton community, while necessarily including attention to taxonomy, have been further extended to explore the general ecology of the organisms encountered. Often considered are such factors as the effects of temperature, light intensity, currents, chemical properties of the water, and the type of substrate on the growth of periphyton. Certain investigators have paid special attention to the development of methods for sampling and analysis of the periphyton community. A review of the literature regarding these general studies may be found in a thesis by Stokes (1969).

Pigment Analysis

The measurement of photosynthetic pigments has been long recognized as a fast and relatively easy method for estimating the productivity of plankton populations. According to Richards and Thompson (1952), the analysis of plankton pigments, when extended to include the various chlorophylls and carotenoids, should yield "(a) a measure of the potential of the plankton for absorbing radiant energy for photosynthesis, (b) some measure of the extent and stage of development of the phytoplankton, and (c) a possible measure of the presence of animals grazing on the crop". The relative concentrations of chlorophylls a, b and c also reflect to a certain degree the composition of an algal community, since members of the various phyla contain different ratios of these pigments. The use of pigment analysis can logically be extended to the determination of the standing crop of epilithic periphyton, and further, to the estimation of the rate of carbon fixation, when assimilation values are known or assumed.

Present evidence suggests that chlorophyll is combined with protein in a lipoprotein complex which also contains the carotenoids, and that the carotenoids may be involved in the photosynthetic reaction. While the involvement of carotenoids in energy transfer for photosynthesis has been questioned by some (Emerson and Lewis, 1942), Dutton and Manning (1941) concluded that light absorbed by some or all of the carotenoid pigments in Nitzschia closterium can be utilized in photosynthesis. Their conclusion was based upon the fact that much of the light at 496 millimicrons is absorbed by carotenoids, yet photosynthetic efficiency is as high at this wavelength as at 660 millimicrons, where chlorophyll alone absorbs light. Wassink and Kersten (1946) showed that fucoxanthin, at least, is active in photosynthesis in Nitzschia dissipata, and Tanada (1951) found the same pigment to be active in Navicula minima. Blinks (1955) has come to similar conclusions regarding certain marine diatoms. When pigment analysis is used for the determination of productivity, then, the carotenoids must be considered. Different ratios and concentrations of various carotenoids are found in algae from different depths in water, and the meaning of these differences in terms of photosynthetic efficiency is not clear. The variation in these pigment concentrations may be due to complementary chromatic adaptation, light intensity adaptation, or both.

According to Guthrie (1928), Willstatter and Stoll were the first to develop a method for the quantitation of chlorophyll in 1913. Guthrie himself developed a colorimetric method in 1928, and prepared a new artificial standard as the basis for quantitation of results. A spectrographic method for the analysis of chlorophylls in ether extracts was employed by Dastur and Buhariwalla, also in 1928. Schertz (1928) described colorimetric and spectrometric methods by which saponified methyl alcohol solutions of chlorophyll could be analyzed. An improved color standard made of organic dyes was introduced in 1930 by Sprague and Troxler. One of the major advancements came when Zscheile (1934) determined quantitatively the specific absorption coefficients of chlorophylls a and b, and developed calculations for the quantitation of mixtures of the two in 90 per cent acetone solution. These calculations removed the necessity for use of a chlorophyll standard in spectrophotometric analysis. Revised formulas for the use of different solvents and for the calculation of degradation products were reported by Zscheile and Comar (1941), Comar and Zscheile (1942), and Zscheile et al. (1942, 1944).

Specific absorption coefficients for various phytoplankton carotenoids were determined in 1952 by Richards. These coefficients, along with estimated values for chlorophyll c, were combined with Zscheile's chlorophyll values in the development of a spectrophotometric method which produced formulas for the calculation of chlorophylls a, b, and c, and astacin and non-astacin carotenoids in plankton samples (Richards and Thompson, 1952). Following the development of a practical plankton concentration method by Creitz and Richards (1955) in which centrifugation was replaced by filtration, the spectrophotometric determination of plankton pigments became rather widespread. To shorten the time required for calculation of results, Duxbury and Yentsch (1956) produced a series of plankton pigment nomographs based on the formulas of Richards and Thompson. The accuracy of Richard's formulas has been questioned by some, including Norman (1957), Parsons (1963), Talling and Driver (1963), and Parsons and Strickland (1963), but suggestions for changes in the formulas have not been consistent. However, Vernon (1960) has presented formulas useful in the calculation of amounts of "inactive" chlorophyll (phaeophytin) in algal communities.[1]

There has been no general concensus on how pigment analyses should be used to estimate productivity. Pigment concentrations may be used simply as an index of standing crop or as a means of estimating the photosynthetic capacity of an algal population. The usual method for phytoplankton is to assume a constant assimilation value for a unit of chlorophyll a at a given light intensity and to multiply the amount of chlorophyll at each depth by the integrated daily photosynthetic rate to give daily production at every depth. The total of these differentials is the total amount of daily production of a column of water with unit area (Saijo and Ichimura, 1961). The use of chlorophyll a was suggested by Gardiner (1943), because chlorophylls b and c are not common to all classes of algae, and they may not be directly active in photosynthesis. This view is not accepted by Humphrey (1961), who notes that chlorophyll a concentrations are not constant from one species to another, are not constant throughout the life cycle, and not constant on a daily or seasonal basis. Margalef (1965) further cautions against the measurement of only chlorophyll a, stating that other absorption bands must also be considered so that community structure may be correlated with changes in productivity. Wetzel (1963) has found poor correlation between C-14 productivity results and chlorophyll concentration because the chlorophyll concentrations are quite variable; thus, the relationship between chlorophyll concentration and assimilation rates must be determined for all environmental conditions. In addition to the variability in pigment concentrations, the assimilation values vary rather widely among different plant populations (Pomeroy, 1961), so values derived for phytoplankton cannot be used for periphyton.

The pigments of lake phytoplankton have been studied on many occasions. The chlorophyll distribution in several Wisconsin lakes was determined by Kozminski (1938). He found that the distribution of chlorophyll with depth is not the same in all lakes, but in many stratified waters, deep-water phytoplankton had up to ten times as much chlorophyll as surface plankton. Manning and Juday (1941), also studying Wisconsin lakes, reported an average production value of seven milligrams of oxygen evolved per hour per milligram of chlorophyll for phytoplankton at optimum light intensity. This figure corresponds to an assimilation value of 2.6 grams of carbon fixed per hour per gram of chlorophyll, somewhat lower than the value of 3.7 grams reported for marine phytoplankton by Ryther and Yentsch (1957).[2] Tucker, in 1949, showed that correlation coefficients for phytoplankton counts and total chlorophyll varied from 0.78 in Lake Erie to 0.97 in laboratory unialgal cultures.

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[1] The conversion of chlorophyll to phaeophytin is accomplished by adding a small amount of concentrated HCl or saturated oxalic acid to an acetone solution of chlorophyll.

Estimations of standing crop of periphytic producers by quantitative measurements of chlorophyll content have been meager. Several workers who used slides as a substrate for attachment of periphyton have estimated standing crop by extracting chlorophyll from a known area. Yount (1956) used the rate of accumulation of chlorophyll on slides as an index of productivity in a study of factors influencing species numbers of diatoms of a Florida spring. Periphyton collected on large plexiglass plates by Grzenda and Brehmer (1960) was removed and the pigments quantitated by a broad spectrum absorption method. Good correlation was observed between pigment units and organic weight. McConnell and Sigler (1959) used large quantities of acetone to extract pigments from periphyton grown on concrete blocks and natural rocks. Results obtained with a broad spectrum colorimeter commonly used in studies of this nature were found to be 15 per cent lower than those derived with a narrow band spectrophotometer (Beckman DU) on which the formulas of Richards and Thompson are based. Using chlorophyll concentrations to estimate the photosynthetic capacity of periphyton colonizing a new substrate, Waters (1961) found that three weeks were required before growth was sufficient to begin to reflect seasonal and successional patterns. In a study of Lake Suwa, in Japan, Hogetsu and Ichimura (1954) brushed periphyton from a standard area on rock surfaces, extracted the chlorophyll and converted it to phaeophytin for photometric analysis. Kobayasi (1961) demonstrated a linear correlation between cell numbers and chlorophyll content of sessile algae from rocks taken from a Japanese river. A study of the pigment content of periphyton growing upon concrete blocks placed in the Blue River, in Oklahoma, was carried out by Duffer and Dorris in 1966. McIntire and Phinney (1965) included pigment analyses in their study of the periphyton of laboratory streams, while Eaton and Moss (1966) determined the pigment content of natural epipelic algal populations. The latter are simply those organisms growing upon sand or mud surfaces.

Photosynthetic Rate Measurement

In addition to the measurement of biomass and the estimation of the efficiency of photosynthetic pigments, it is desirable to actually measure as nearly as possible the instantaneous production rate of an algal community. For this, one must turn to the reactions involved in organic production and the accompanying chemical changes which may be detected by more sensitive means. In photosynthesis, carbon dioxide is reduced to organic carbon with the evolution of free oxygen, the reaction utilizing the energy of solar radiation. Early physiological investigations showed that the volume of oxygen liberated during photosynthesis very nearly approximates the volume of carbon dioxide assimilated. It has been assumed that the primary product of photosynthesis is carbohydrate in nature and that the following simplified equation for the overall reaction applies:

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[2] Assimilation value is defined as grams of carbon fixed per hour per gram of chlorophyll (synonyms -- assimilation number, assimilation ratio).

$$CO_2 + H_2O \dashrightarrow CH_2O + O_2$$

Even though it has been shown that the oxygen is derived not from carbon dioxide but from water, requiring a modification of the equation to satisfy the stoichiometry, the proportions of the constituents remain the same; the measurement of either carbon dioxide assimilated or oxygen evolved during a given time period yields an accurate picture of the production rate of a community.

Gaarder and Gran (1927) first used the light and dark bottle method for determining oxygen changes during photosynthesis and respiration in phytoplankton communities in situ. This method was also used extensively by Riley (1940) in his investigations of aquatic productivity. Steeman-Nielsen (1952) modified the light and dark bottle technique for the measurement of radioactive carbon assimilation. Many workers have used the Warburg apparatus to determine manometrically the photosynthetic rates of algal cultures in the laboratory. However, this method is rather tedious due to the necessity for calibration of glassware. Gilson (1963) designed a differential respirometer which operates at ambient pressure and produces a direct digital readout in microliters of gas evolved or absorbed. This respirometer has greatly reduced the time required to determine photosynthetic and respiratory rates of algal communities.

Many basic laboratory studies have been conducted to establish the relationships between pigment concentrations, light intensity, temperature, and the photosynthetic and respiratory activity of different types of plant communities. In 1918 Boysen-Jensen found the compensation point (light intensity at which P/R=1) to be five times lower in shade adapted plants than in light adapted plants, yet the productivity of shade plants was considered to be lower than light plants. Emerson (1929a, 1929b) reported that photosynthesis in Chlorella vulgaris reaches its maximum rate at about the same light intensity over a range of different chlorophyll concentrations, and that the magnitude of the rate is a smooth function of chlorophyll content. A similar observation was made by Fleischer (1935), but no correlation was seen between respiration and chlorophyll content. It was later shown by Emerson et al. (1940) that the ratio of moles of chlorophyll present to moles of CO_2 reduced is not a constant in Chlorella pyrenoidosa, but depends on conditions of previous growth, increasing sharply with age of the culture and varying with color and intensity of culture illumination. Sargent (1940) states that Chlorella pyrenoidosa cultivated under intense illumination has a low chlorophyll content and a high capacity for photosynthesis, but when cultivated under moderately low illumination it has a high chlorophyll content and a low capacity for the Blackman reaction.

The effect of the past history of cells of Chlorella on their photosynthetic capacity was studied by Sorokin (1958). He found that both the temperature and light intensity maintained during growth had profound effects on the rate of photosynthesis measured under a variety of conditions. McAllister et al. (1964) suggest that at low light intensities, kinetic control depends only on the energy of illumination and the total number of molecules of all pigment types, and is largely independent of the physiological condition of the organism. However, at high light intensities, the photosynthetic rate seems more related to chlorophyll a concentration than to total pigments or a combination of a few pigments.

When gross photosynthesis is calculated on the basis of net photosynthesis and respiration data, the prime assumption is that respiration occurs at the same rate in both light and dark. Several investigators, including Emerson and Lewis (1943), have conducted studies purporting to show that respiration is lower in light than in dark. However, when measuring photosynthesis and respiration of green algae at the same time in alternate light and dark with a mass spectrometer, Brown (1953) found that respiration did not decrease during the light period. Brown and Webster (1943) had earlier shown the same to be true for blue-green algae. As pointed out by Brackett et al. (1953), it is possible for respiration to appear lower in light than in dark when very short periods of illumination are used, due to a preferential reutilization of photosynthetic oxygen by the cells. Therefore it is desirable to allow a sufficient period of equilibration before making manometric readings when periods of light and dark are alternated.

Oxygen tension was shown by Gessner and Pannier (1958) to be a significant factor in the respiration rates exhibited by algal cultures. Respiration rates were found to double when the oxygen tension was increased from 100 per cent saturation to 400 per cent saturation. In two rare laboratory studies of note relating to the respiration of periphyton organisms (McIntire, 1966, 1968), it was shown that increased oxygen tension always produced an increased respiratory rate regardless of other environmental conditions. According to Wetzel (1965), Felfoldy has used manometric techniques to determine the photosynthetic rates of some natural periphytic communities under laboratory conditions. Several measures of biomass were found to be poorly correlated with photosynthetic rates.

Field studies aimed at primary production measurement by determining photosynthetic rates have been numerous, but usually have been restricted to the investigation of phytoplankton. Much of the early work relating photosynthesis and light intensity was summarized in 1936 by Smith. Marshall and Orr (1928) used the bottle method to measure the photosynthetic rate of diatom cultures at various depths in the sea. They found the compensation point at about 20-30 meters in Loch Striven. Simultaneous measurement of photosynthesis in tropical ocean waters using the C-14 method and the light and dark bottle oxygen technique was performed by Ryther (1954). The C-14 method was said to produce results 10 to 100 times lower than the oxygen technique, due probably to preferential respiration of newly-formed products of their photosynthesis by the algae. Later studies (Ryther and Vaccaro, 1954; Ryther, 1956; Ryther and Yentsch, 1957; and Yentsch and Ryther, 1957) indicated that the oxygen method and the C-14 method produce favorably comparable results.

The problem of light adaptation by algae has received the attention of several researchers, including Ryther and Menzel (1959), who studied the photosynthesis of phytoplankton at the surface, and at ten and one per cent light penetration levels in the Sargasso Sea. In the winter, the plankton at all three depths behaved like "sun" forms, becoming fully light saturated at 5000 foot-candles. In the summer, when the water and the plankton were stratified, those at the one per cent level behaved like "shade" plants (light saturation below 1000 foot-candles), while those at the surface reacted as in winter. This adaptation was said to affect the calculation of productivity based on chlorophyll and light data. Steeman-Nielsen and Hansen (1959) and Talling (1960) have shown the compensation point to be much higher for algae adapted to a high light intensity than those adapted to a low intensity. Since light adaptation appears seasonally and spatially, Saijo and Ichimura (1961) believe that photosynthesis-light curves must be developed for each sampling area under consideration and that these curves must be modified to account for differing conditions. Ichimura (1960) has shown that the effects of past environmental conditions on algae do not hold for long periods, and are important only when the populations are stratified in some manner. The effects of such factors as temperature and photoperiod on the photosynthesis-chlorophyll-light relationships have been considered by Doty and Oguri (1957), Shinada (1958), Curl and Small (1965), and Williams and Murdock (1966).

Important studies regarding the photosynthetic rates of plankton in lakes have been carried out by Manning et al. (1938) and Manning and Juday (1941). Manning and Juday reported that production in Wisconsin lakes varied from fourteen to forty-four kilograms of glucose per hectare per day. Many investigations of phytoplankton productivity in lakes have been reported by Verduin (1953, 1954, 1956, 1957, 1960). According to his calculations, the mean photosynthetic rate of lake phytoplankton under optimal light intensity is about 0.5 micromoles of oxygen evolved or carbon dioxide consumed per microliter of organisms per hour; one to two micromoles per milligram ash-free dry weight per hour; and 0.2 micromoles per microgram of chlorophyll per hour. Computations for several lakes yielded values lying between 150 and 200 millimoles of oxygen per square meter per day. Juday (1940) calculated that the organisms of Lake Mendota utilized 0.35 per cent of the available light energy during an entire year. Reported maximum instantaneous efficiencies in the marine environment range from 1.6 per cent (Ryther et al., 1958) to 7.0 per cent (Jenkin, 1937).

Field investigations of the photosynthetic activity of periphyton communities have been rare. Odum (1956, 1957), Park et al. (1958), and Hoskin (1959) included periphytic algae in their studies of stream metabolism. Pomeroy (1959) estimated the photosynthesis of salt marsh algae by the light and dark bell jar oxygen method, where the jars were filled with boiled, filtered water. Significant oxygen changes within an hour were reported. The productivity of exposed algae during low tide was estimated by a flowing-air system with CO_2 absorption columns. In a mountain stream, Kobayasi (1961) removed sessile algae by hand, then homogenized and suspended this material in bottles of river water. Productivity was estimated by the standard light and dark bottle oxygen technique. Light intensity was regulated by a graded series of neutral density filters. Periphytic algae which were adapted to low light intensities reached maximum photosynthetic rates at relatively low intensities. A similar technique has been used by McConnell and Sigler (1959) to determine the productivity of periphyton from a swift river in Utah. The only reported investigation relating to the photosynthesis of Great Lakes periphyton is that conducted by Jackson (1966). His study involved the use of the light and dark bottle oxygen technique to determine photosynthetic rates of Cladophora in Lake Ontario. There are several problems associated with the bottle method for measurement of periphyton productivity, including the fact that pH, carbon dioxide concentration, and oxygen tension cannot be held constant. Another problem, borne out by the work of Whitford (1960) and Whitford and Schumacher (1961), is that the bottle technique generally produces an underestimation of productivity, since water movement is restricted by this method.

MATERIALS AND METHODS

The first phase of the productivity study involved field studies in which the biomass, production rates and regrowth capabilities of naturally occurring periphyton in selected areas of Lake Superior were quantitated and analyzed on the basis of pigment concentrations, photosynthetic rates, and other parameters. The second phase was a laboratory study in which the effects of light intensity and temperature on pigment concentrations and photosynthetic rates of periphyton were determined experimentally. Most of the samples for both phases of the investigation were taken from a selected area within the confines of Stony Point Bay. This bay is situated on the western arm of Lake Superior near Duluth, Minnesota, fifteen miles northeast of the University of Minnesota Limnological Research Station at Lester River. The northeastern boundary of the study area is Stony Point, while the mouth of the Little Sucker River serves as the southwestern boundary. Two miles to the north, at Knife River Harbor, the research vessels _Oneota_ and _Jacobs_ are moored.

Stony Point Bay was surveyed to establish depth contours and to determine the total area of the bay, thus providing a basis for subsequent quantitative calculations of productivity in the periphyton community. The details of this survey are reported elsewhere (Fox, 1969); however, since measurements taken at that time are employed in the calculation of certain results in the present study, the basic procedures involved in the survey will be reviewed here. The shoreline contour was determined by the use of a professional transit and stadia rod. After a baseline was established on the shore, the relative positions of points along the shoreline between Stony Point and the Little Sucker River were determined by triangulation and plotted on a master map. These observations provided the basis for a shoreline drawing. For the determination of depth contours, a reference buoy was placed in the bay, 2336 feet to the south of a base station on the shore. The area delineated by the shoreline from Stony Point to the Little Sucker River and from those points to the reference buoy was considered to be the total area of the bay. Depth readings were made with an electric fathometer aboard the _Oneota_ as the vessel traversed the bay. As each depth sounding was made, the position of the _Oneota_ was determined by use of the transit on shore and a stadia rod aboard the vessel. In shallow areas, depth readings were made with a sounding pole from a small dinghy. When depths were plotted on the master map, points of equal depth were connected to depict the depth contours. The type of bottom, i.e., rock or sand, was determined in shallow water by observation with a water glass. Where the water was too deep for this procedure, SCUBA divers made observations of bottom type.

Procedures, 1966

Routine sampling of natural periphyton from Stony Point Bay began during the summer of 1966. The samples were taken at depths of 2.5, 5, 10, 15, 20 and 35 feet along a course perpendicular to the shoreline; each sampling station was marked permanently with an anchored buoy. Divers and sampling equipment were transported on the Oneota from Knife River Harbor to Stony Point Bay, where the vessel was anchored at the thirty-five foot station. Divers employing SCUBA techniques obtained three rocks of four to six inch diameter from each of the six sampling depths. Each diver carried a plastic bag over his right hand and forearm as he dived to the sampling area. Upon grasping a rock with his right hand, he pulled the plastic bag down over his forearm and hand, enclosing the rock with its attached periphyton within the bag. The samples were carried to the surface and handed to a person aboard a small boat, whereupon the bags were knotted and placed in plastic buckets for transport to the laboratory. Water samples were also taken near the bottom at each station to determine the magnitude of error resulting from the inclusion of phytoplankton in the small amount of water accompanying each rock in the plastic bag. Samples were usually taken between 10:00 A.M. and noon, and were carried to the laboratory by automobile within three hours.

In the laboratory, the bags were placed in small tubs and cut open with a scalpel. The periphyton was then removed from the rocks with a plastic brush. Small quantities of distilled water were used to rinse loosened periphyton from the rocks and bags. The materials taken from all three rocks from a given sampling point were combined, yielding an immediate "average mixture" for that station. The area on each rock where periphyton had been attached was marked by scraping a line around the rock with a dull scalpel. After the volume of a sample had been measured in a graduated cylinder, the slurry was transferred to a small plastic bucket. While the suspension was mixed by vertical movement of an inverted funnel, aliquots were pipetted for pigment analysis, identification and enumeration of organisms, and for photosynthesis, volume, and weight determinations.

Measurement of the denuded surface areas of the rocks was accomplished by lubricating the previously marked area with automobile grease and coating it with melted paraffin. Heated paraffin was applied to the rock with a paint brush until a 1/8 to 1/4-inch layer was formed. When the paraffin was hardened, yet still pliable, it was incised in such a way that it could be removed and placed as a single flat layer on a piece of heavy paper. The outline of each paraffin model was traced on the paper and the total area covered was determined by retracing the outline with a previously calibrated polar planimeter. The measurements of the three rocks from each sampling station were totaled to produce the basis for quantitative calculation of results.

For the analysis of periphyton pigments in samples taken during 1966, twenty-milliliter aliquots of suspension were removed from each sample. When the suspension appeared less turbid than usual, a forty-milliliter aliquot was used. These aliquots were processed according to a modification of a pigment extraction method suggested by Creitz and Richards (1955) for the analysis of phytoplankton. The detailed procedure is as follows. Each portion of periphyton suspension was filtered through a glass fiber filter (Gelman, Type A), and the collected material was fixed by washing with fifteen milliliters of saturated magnesium carbonate solution. The purpose of this washing was to provide buffering and thus prevent the conversion of chlorophyll to phaeophytin. Each filter was ground in a tissue grinder along with five milliliters of ninety percent reagent-grade acetone to effect pigment extraction. The material was transferred to a graduated centrifuge tube and the volume was adjusted to ten milliliters with acetone. The suspension was then centrifuged in a stoppered tube for ten minutes to produce a clear supernatant solution from which a five-milliliter aliquot was pipetted into a cuvette. Total chlorophyll was first estimated on the basis of readings made with a Klett-Summerson colorimeter, using a No. 66 Klett-Summerson filter (640-700 millimicrons) and ninety percent acetone as the zero absorption standard. The following formula was used to calculate total chlorophyll concentrations:

$$\text{Chlorophyll (Mg/cm}^2\text{)} = \frac{(0.28)\ (\text{Klett units})\ (2)\ (\text{L. of sample})}{10^3\ (\text{L. of aliquot})\ (\text{cm}^2\ \text{surface area})}$$

Results are expressed in terms of milligrams of chlorophyll per 100 square centimeters of rock surface and as milligrams of chlorophyll per 100,000 organisms.

Each of the pigment solutions tested in the K-S colorimeter was then transferred to an absorption cell and its spectrum from 350 to 700 millimicrons was scanned and plotted with the Beckman DK-2A spectrophotometer, again using ninety percent acetone as the reference. The ratio of reference to sample absorbance (R/S) of a split-beam single light source is plotted by the instrument, thus removing any error accountable to unexpected power modulation. Sample temperature was held constant at 30° C. by means of a control device mounted on the instrument. Absorbance values at wavelengths of 480, 510, 630, 645 and 665 millimicrons were taken from the charted data and used for calculation of chlorophyll a, b and c concentrations, as well as for calculation of astacin and non-astacin carotenoids. The formulas developed by Richards and Thompson (1952), which were used in these calculations, are shown below.

Chlorophyll a (mg/L) = $15.6D_{665} - 2.0D_{645} - 0.8D_{630}$;
Chlorophyll b (mg/L) = $25.4D_{645} - 4.4D_{665} - 10.3D_{630}$;
Chlorophyll c (MSPU) = $109D_{630} - 12.5D_{665} - 28.7D_{645}$;
where D is absorbance at a given wavelength.
$D_{res}, 510 = D_{510} - .0026C_a - .0035C_b - .0021C_c$;
$D_{res}, 480 = D_{480} - .0019C_a - .0136C_b - .0054C_c$;
where D_{res} is the residual absorbance at a given wavelength after subtraction of the absorbancies of the chlorophylls.
Astacin carotenoids (MSPU/L) = $2(4.45D_{res}, 510 - D_{res}, 480)$
Non-ast. carotenoids (MSPU/L) = $7.6(D_{res}, 480 - 1.49D_{res}, 510)$

Results are converted to milligrams (or MSPU) of pigment per 100 square centimeters of rock surface, and to milligrams (or MSPU) per 100,000 organisms at various sampling depths.[3]

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[3] MSPU = millispecified pigment unit. It represents a specific, but undetermined, weight of the pigment which should be about one milligram, based on the weights and absorption coefficients of related compounds (Richards and Thompson, 1952).

A Gilson differential-volumetric respirometer was used to determine the gross photosynthetic rate of the periphyton. This instrument measures volume changes as a gas is absorbed or evolved under constant temperature and pressure, producing a digital reading directly in microliters. A special cover of black plastic sheeting was constructed for the respirometer so that the respiration rate of periphyton organisms in total darkness could be determined. The instrument is equipped with a bank of floodlights to facilitate photosynthesis measurements. Four-milliliter aliquots of the periphyton-water suspension were pipetted into acid-cleaned Warburg flasks together with 1.92 milliliters of carbonate-bicarbonate buffer solution (Warburg Number 11). This solution is composed of 0.1 molar sodium bicarbonate (95 percent) and 0.1 molar potassium carbonate (five percent). The buffer insures a constant pH (8.2), provides an adequate carbon dioxide source for photosynthesis, and incorporates carbon dioxide evolved during respiration into the carbonate-bicarbonate system. The reaction flasks were attached to individual manometers, each of which was connected to a common reference flask. A mixture of five per cent carbon dioxide in air was introduced into the gas spaces above the samples. The flasks were shaken in a 20° C. water bath while manometer readings were made during alternate ten minute light (1500 foot-candles) and dark periods. A ten-minute equilibration interval was allowed before each light or dark test.

During the light periods, both photosynthesis and respiration occur, and manometer readings reflect net photosynthesis (oxygen evolution less oxygen absorption, or "P+R"). In the dark, only respiration occurs. The manometer readings, therefore, indicate oxygen absorption, or "R". The assumption was made that oxygen absorption (respiration) in the dark is volumetrically equal to absorption in the light. Therefore, gross photosynthesis rate could be determined on the basis of the formula P (ten minutes) = $-[R-(P+R)]$ (from Umbreit, et al., 1964). A correction factor involving barometric pressure and water vapor pressure was applied to yield microliters of dry gas at 760 millimeters of mercury. The results of three separate runs on each sample were averaged and expressed as microliters of oxygen produced per hour per 100 square centimeter of rock surface, and as microliters per hour per milligram of total chlorophyll.

Dry weights were determined by filtering four-milliliter portions of the periphyton suspensions through pre-weighed membrane filters; each filter, with its collected material, was dried for one hour in an oven at 103° C. and weighed again. Results are expressed as milligrams per square centimeter of rock surface.

Periphyton volume was estimated by settling the material from forty milliliters of suspension for three hours in a narrow graduated cylinder. Thus the recorded volumes included small and varying amounts of sand and clay. Results are reported in terms of milliliters of periphyton per square centimeter of rock surface.

Identification and enumeration of organisms collected during the 1966 season were performed and reported by Fox (1969). The total counts reported by him have been used in the present study only to calculate pigment concentrations on the basis of a standard number of organisms. For counting, a twenty-five milliliter aliquot was transferred to a sample bottle along with twenty-five milliliters of ten percent formalin. One milliliter of this suspension was pipetted into a Sedgwick-Rafter counting cell and allowed to settle for ten minutes. A binocular compound microscope fitted with a Whipple disc was used to count ten random fields at a magnification of 200 diameters. The total numbers of organisms per square centimeter of rock surface for all samples were used for calculation of milligrams of pigment per 100,000 organisms.

Procedures, 1967

Field studies were continued during the summer of 1967 (June 9 to September 15) with accelerated routine sampling of the naturally occurring periphyton of Stony Point Bay. Three rocks were taken twice each week from sampling stations at 2.5, 5, 10, 15, 20 and 35 foot depths. Water temperature and light intensity readings were recorded during each sampling run. The temperature of water near the bottom at each sampling station was determined by a diver carrying a standardized laboratory thermometer. Light intensity at each depth was measured with a GM submersible photometer. In addition, daily incident radiation was continually recorded during the summer by a photometer situated on the roof of the laboratory.

A study of the rate of establishment of periphyton in Stony Point Bay was initiated in June, 1967. In order to present natural conditions for growth, rocks from the bay itself which were already supporting periphyton growth were chosen for use as a substrate in the regrowth experiment. This natural substrate was chosen to avoid the deviations in growth which may be expected with the use of an artificial substrate. Rocks of four to six inch diameter were obtained from shallow water in the bay and transported to the laboratory, where they were scrubbed free of periphyton with a plastic brush and rinsed with tap water. The rocks were then autoclaved for twenty minutes at a pressure of fifteen pounds per square inch (250°F.). After sterilization, the rocks were replaced in Stony Point Bay at depths of 10, 20, and 35 feet by SCUBA divers. The rocks were lowered in a wire basket to the divers, who placed them on the bottom in a circle around the anchor for a marker buoy. After predetermined "incubation" periods, ranging from eight hours to 101 days, three rocks were retrieved from each depth by divers employing the plastic bag technique.

In addition to the regular sampling of Stony Point Bay, an investigation of the periphyton of other north shore areas was carried out during the summer of 1967. Eleven stations approximately ten miles apart along a 107 mile segment of the north shore of Lake Superior were selected for sampling of the periphyton community. These stations ranged from the southernmost at Lester River to the northernmost at Grand Marais, Minnesota. A fourteen-foot aluminum boat equipped with a five horsepower outboard motor was towed by automobile to each sampling area. Each station was sampled on two different days by SCUBA divers employing the same techniques used in Stony Point Bay. Depths were determined with previously calibrated pitot-tube depth gauges carried by the divers. Temperatures were taken at the surface and near the bottom at each sampling location. Three rocks were taken from depths of 2.5, 5, 10, 15, 20 and 35 feet except in certain cases where no rocks were encountered at the 35 foot depth.

Sketch maps showing the shoreline and prominent landmarks at each sampling station were developed to indicate the line along which samples were taken. With the exception of Lester River, Tofte, and Grand Marais, the general procedures used in developing these maps were the same as those employed to determine the shoreline contour of Stony Point Bay. From either end of an established baseline, the angle formed between a north-south line and several landmarks along the shore were established with a transit. The length of the baseline was determined with a transit and a stadia rod. After the baseline had been drawn to scale, the shoreline points were plotted by triangulation.

Because the terrain was too rough to establish a baseline at either Lester River or Tofte, a single base station was selected at each of these locations and its position determined in relation to certain landmarks. From this station, angles and distances to selected points along the shore were established with the transit and stadia rod. These values were used to plot and connect the points on graph paper, thus producing a scaled drawing of the shoreline. The map of the Grand Marais area was traced from a U.S. Corps of Engineers chart (#97).

Samples collected from Stony Point Bay and the other north shore stations during the summer of 1967 were prepared for laboratory examination by the same basic procedures as described previously. Pigment analyses were performed on all samples in the same manner as in 1966, except that the K-S colorimeter was not used to estimate total chlorophyll. Photosynthetic rate under standard conditions was again determined for each sample from Stony Point Bay. Since the addition of carbon dioxide to the reaction flasks seemed to pressurize the system and produce high results, none was added during the 1967 measurements. Due to the large number of samples collected in a short period of time from the other north shore stations, photosynthetic rates of only a limited number of these samples could be determined.

In addition to the determination of total dry weights, the samples were analyzed for ash-free (organic) dry weight. A twenty-five milliliter aliquot of each periphyton suspension was drawn through a pre-weighed four-centimeter filter paper. The filters were placed in pre-weighed porcelain crucibles and dried for one hour in an oven at 103°C. After the crucibles had been cooled in a desiccator and reweighed, they were placed in a muffle furnace at 600°C. for fifteen minutes. After cooling in the desiccator, the ashed samples were weighed again for the calculation of ash-free dry weights. Results are expressed as milligrams of total dry weight and ash-free dry weight per square centimeter of rock surface.

Identification and enumeration of organisms were again carried out and reported by Fox (1969). As in 1966, the total counts from his study were utilized for the correlation of counts with the parameters examined in this study.

Procedures, 1968

The second phase of the investigation, which began in June, 1968, was designed to provide information regarding the effects of short-term changes in light intensity and temperature on the productivity of Lake Superior periphyton. The general procedure was to "condition", or acclimate, natural periphyton samples to various light intensities and temperatures for short periods in the laboratory and then to determine the photosynthetic rates of the conditioned samples in crossed gradients of light intensity and temperature. Analysis of photosynthetic pigment concentrations in conditioned samples allowed the calculation of assimilation values for periphyton organisms under a variety of conditions. The rate of change of pigment concentrations following an increase or reduction of light intensity was also examined.

To facilitate the conditioning of periphyton organisms in a simulated lentic situation, special incubators were designed for use in the laboratory. Each of four Precision B.O.D. incubators with variable temperature control was modified to enclose a ten-liter plastic tub which served as a sample container. Two banks of fluorescent lamps (General Electric daylight white, 20 inch) were mounted in a vertical position along the inside walls of the incubators. The light intensity within the incubators could be altered by adding, removing or masking lamps in the lighting system. A Weston light meter reading directly in foot-candles was used to measure light intensity in the incubators. A continual-flow water circulation system was installed in each incubator for the purpose of maintaining a steady, slow flow of water through the sample container. A variable-speed peristaltic pump mounted on the top of the incubator circulated water through the sample container by means of 3/8-inch Tygon tubing. The inlet and outlet tubing reached from the pump to the sample container through two small holes drilled in the side of the incubator. The inlet tube reached slightly below the surface of the water in the container, while the outlet tube was anchored to the bottom in the opposite corner of the container. A four-liter plastic aspirator bottle was suspended above the sample container inside the incubator and tied into the inlet line. This bottle could be disconnected and removed at selected intervals and replaced with another bottle full of fresh water, thus serving as a means for maintaining a rather constant level of nutrients in contact with the samples.

Rocks with well established growths of periphyton were carefully collected by hand from Stony Point Bay and placed in buckets of water for transport to the laboratory. The rocks were transferred to the sample containers in the incubators. Water from Stony Point Bay was collected daily in a large carboy and used as the medium for sustaining growth of the samples in the containers; the rocks were submerged in seven liters of water. To simulate the lentic situation, the pumps were arbitrarily set to recirculate the water at a rate of 350 milliliters per minute. This rate allowed a retention time of twenty minutes in the sample container. During all experiments, the medium was partially changed each day by replacement of the aspirator bottle.

Plate Number 1 provides an exterior view of the incubators, showing the position of the water pumps and individual ballasts for each fluorescent lamp. These components were located outside the incubators in order to disperse the heat developed during operation. The interior of an incubator is shown in Plate Number 2. The position of the sample container, the fluorescent lamps, and the aspirator bottle may be seen. Plate Number 3 provides a close-up view of a rock with attached periphyton which had been transported from Stony Point Bay to the laboratory and placed in an incubator.

Four different sets of conditions for incubation could be provided at one time by selecting various combinations of temperature and light intensity within the incubators. After a specified time period, the rocks were usually removed from the incubators and the attached periphyton removed for analysis as previously described. Pigment analyses and ash-free dry weight determinations were performed as in the field study. Organisms were microscopically examined, counted and identified to species if possible. For the determination of photosynthetic rates under different conditions, it was necessary to alter the respirometer so that various light intensities could be produced. This was accomplished by removing certain lights from the apparatus and positioning the flasks in such a way as to provide different light intensities at nine flask locations (20, 60, 80, 180, 300, 400, 600, 900 and 1500 foot-candles). These intensities were determined with the Weston light meter. Photosynthetic rates of conditioned samples were measured at the nine light intensities and at a variety of temperatures by employing the automatic water bath temperature control on the respirometer.

Several different experiments were run during the second phase of this investigation, each designed to examine a separate problem and each employing the general procedures described above. These experiments will be discussed separately in a section to follow.

Plate 1

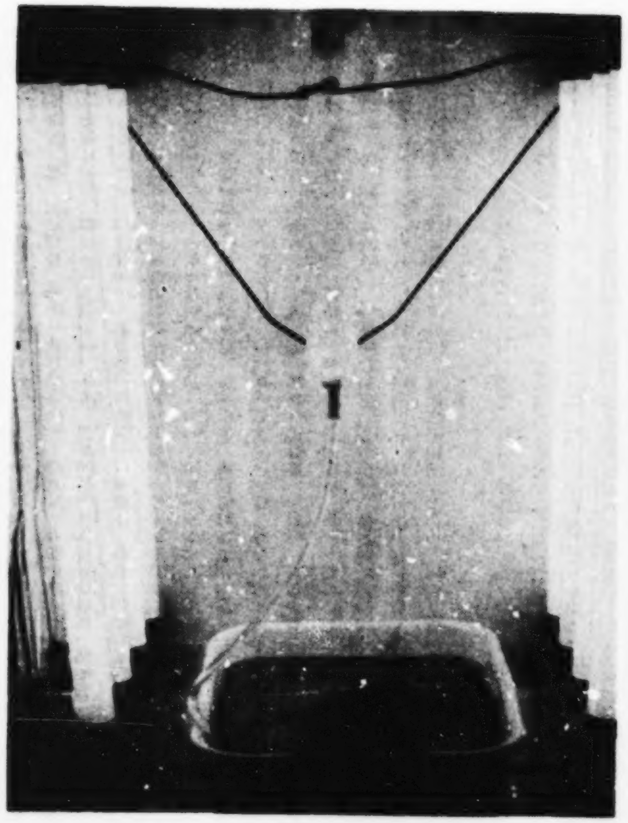

Plate 2

Plate 3

RESULTS AND DISCUSSION

Since the sampling was carried out during three consecutive summers, the results of this investigation are presented in chronological order. While some quantitative data were obtained in 1966, this period was spent mostly in the development of methods. Each year certain changes were made to improve field and laboratory techniques, and these changes are reflected in the data. The most comprehensive sampling program was conducted during the summer of 1967, when, in addition to routine sampling of Stony Point Bay, the periphyton of other areas as far north as Grand Marais, Minnesota was examined. Certain questions regarding the dynamics of Lake Superior periphyton arose during the examination of data acquired during 1966 and 1967. In 1968, laboratory experiments were designed to answer these questions. The results of these laboratory experiments were needed to convert the data collected earlier under standard conditions to a form more nearly approximating the actual situation in the lake.

In the interest of brevity and clarity, this chapter includes discussion of results along with the presentation of data. The data have been combined and summarized in various ways and are presented in the form of figures and tables. The discussion involves general interpretation of the data, comparisons between results of the three summers and between various sampling areas, and correlations between the several parameters employed in the study of periphyton. When possible, results will be compared with data reported from other studies of periphyton communities. An attempt also will be made to establish the relative importance of the periphyton community as a primary producer in Lake Superior when a comparison is made with the productivity of the phytoplankton.

I. DESCRIPTION OF STONY POINT BAY

The relative position of Stony Point Bay on the western arm of Lake Superior is indicated in Figure 1. Figure 2 is a detailed representation of the sampling area, showing the shoreline contour, depth profiles, and bottom types. Most of the bottom area was covered by rocks, with only very small scattered sand patches; the portion of the bay floor designated by the word "sand" in Figure 2 was predominantly sandy, although several small patches of rocks were encountered in this area also. The rocks ranged in size from one inch to five or six feet in diameter, but most of the bottom was covered by rocks ranging from four to twelve inches in diameter. The triangular sampling area, bounded by the reference buoy 2336 feet from shore, the Little Sucker River on the southwest, and Stony Point on the northeast, was found to encompass 321,000 square meters.

Stony Point Bay is located in a sparsely populated area and is not easily accessible from the adjacent land because the banks leading to the water's edge are very steep. The only persons encountered in the bay were commercial fishermen who came by boat to tend small

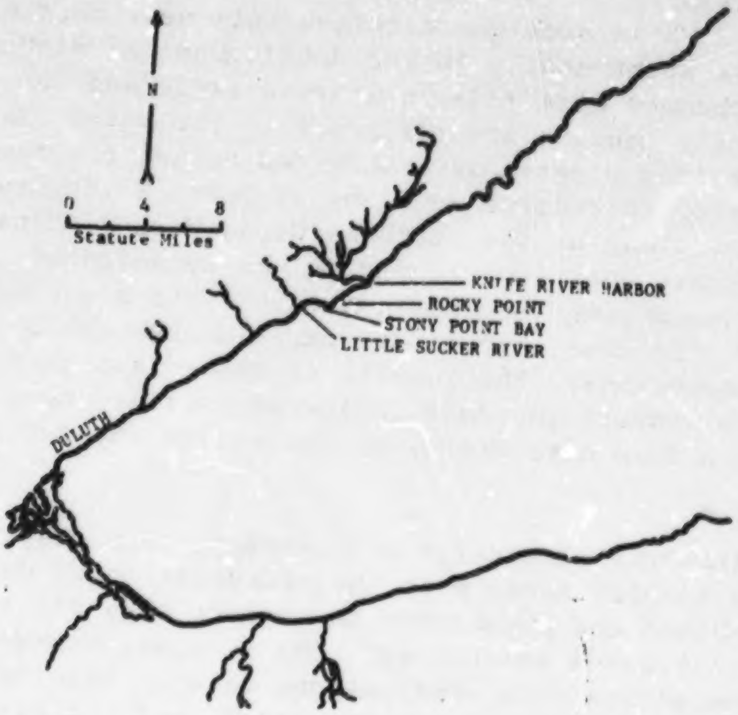
N
0
4
8
Statute Miles
KNIFE RIVER HARBOR
ROCKY POINT
STONY POINT BAY
LITTLE SUCKER RIVER
DULUTH

Figure 1. Western Arm of Lake Superior, Showing the Position of Stony Point Bay, Site of Periphyton Studies.

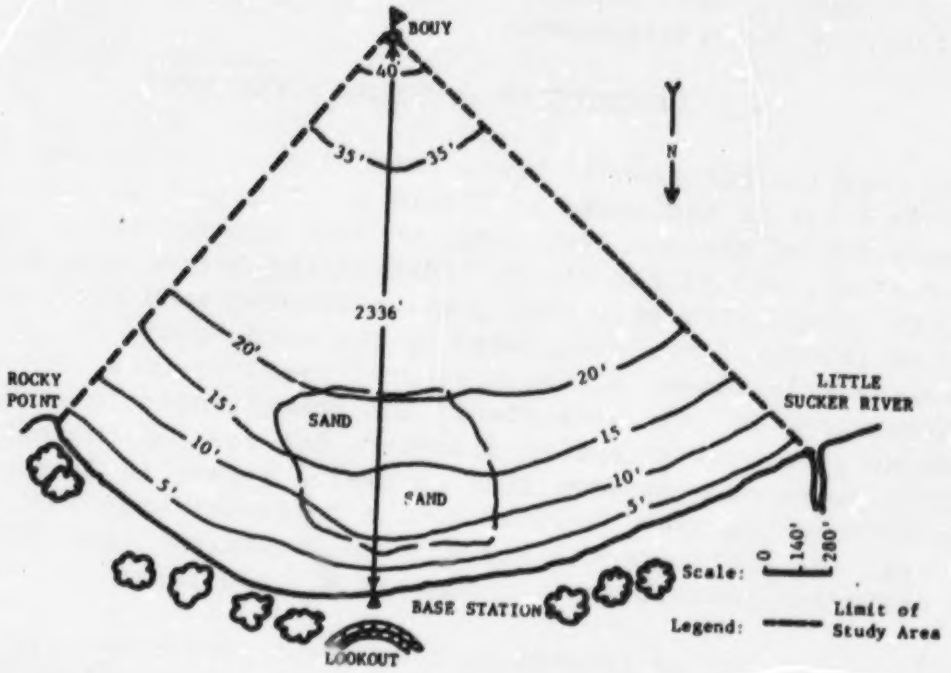
BOUY
40'
35'
35'
N
2336'
20'
20'
ROCKY POINT
LITTLE SUCKER RIVER
15'
15
SAND
10'
10'
SAND
5'
5'
Scale:
0
140'
280'
BASE STATION
LOOKOUT
Legend:
Limit of Study Area

Figure 2. Detailed Map of Stony Point Bay, Lake Superior.

fishnet cribs which are permanently located in the bay. The fishermen expressed an interest in the periphyton project, as they often find their nets fouled by profuse growths of organisms.

Turbidity in the water of the bay was quite variable and was considerably affected by flow from the Little Sucker River. During and following stormy periods, heavy suspensions of silt were carried into the bay from the mouth of the river, whereupon the material was often carried across the bay in an easterly direction.[4] Periphyton organisms and silt from the shore area were also suspended in the bay when wave action was severe. Secchi disc readings varied considerably, the maximum being approximately eight meters. Occasionally, the water was clear enough that the bottom could be viewed from the surface in depths up to twenty feet. Water color as viewed from shore was usually greenish, but atmospheric conditions and turbidity sometimes accounted for a tan or grey appearance.

A heavy, brown layer of periphyton was usually apparent on the rocks and sand in the bay. Where the periphyton was not disturbed by wave action, small gas bubbles could be seen entrapped in the wooly growth. Occasionally, divers reported viewing small fish near the bottom of the bay; these fish were found to be sculpins (genus Cottus). Small groups of crustaceans, identified as Mysis relicta, were sometimes present. Mayfly nymphs, midge larvae, caddisfly larvae, nematodes, snails and leeches were found in association with the periphyton on the rocks. A few clumps of the macroscopic, filamentous green alga, Nitella, were encountered on rare occasions.

The rocks taken from Stony Point Bay differed somewhat from one another in appearance when the periphyton was removed. An analysis of one hundred of these rocks revealed that twenty-two lithic types were represented in the bay (Table I). The predominant type was found to be basalt (fifty-six per cent), of which twenty-four per cent were andesite (sixteen per cent) and diabase (eight per cent). Fourteen of the one hundred were diabase, while seven were porphyritic trachyandesite to mafic quartz latite.

II. 1966 FINDINGS

Data presented are taken from that portion of the study carried out between August 9 and September 6. During this twenty-nine day sampling period, east or northeast winds occurred on eleven days, or thirty-eight per cent of the time. The average velocity was fifteen miles per hour. These winds caused very rough water, making it impossible to safely navigate the two miles from Knife River Harbor to Stony Point Bay. For this reason, only five sampling trips were completed. However, in the course of these five trips, a total of eighty-one rocks were obtained from depths of 2.5, 5, 10, 15, 20,

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[4] Ruschmeyer and Olson (1957) have shown the general circulation of water in the western arm of Lake Superior to be counterclockwise. However, winds and eddy effects can cause a reversal of flow near shore in certain areas.

TABLE I

LITHIC DESCRIPTION OF ROCK SAMPLES FROM STONY POINT BAY, LAKE SUPERIOR

Number of samples	Lithic description
2	medium to coarse gr. granitic rocks
1	porphyritic andesite
1	massive graywacke
1	laminated hornfels, pelitic
2	fine gr., porphyritic, red granophyre
10	aphanitic to very fine gr. basalt, aphyric
2	very fine gr., basalt with small amygdules
16	very fine gr., porphyritic basalt or andesite
7	very fine gr., porphyritic trachyandesite to mafic quartz latite (intermediate)
2	fine gr., porphyritic trachyandesite
1	very fine grained porphyritic felsite
6	fine gr. to fine- to med. gr. amygdaloidal basalt
11	aphanitic to very fine grained ophitic basalt
3	fine grained ophitic basalt
8	fine to med. grained basalt or diabase
6	fine grained diabase (intrusive)
14	fine to medium grained diabase
2	anorthositic gabbro
1	anorthositic olivine gabbro
1	porphyritic gabbroic anorthosite
2	arkosic sandstone (one red, one white)
1	red siltstone
100	

and 35 feet in Stony Point Bay.

The average periphyton pigment concentrations per unit area of rock surface are plotted against sampling depth in Figure 3. Maximum, minimum, and mean concentrations are presented in Table II. Since the quantity of phytoplankton pigments, in the small amounts of water collected along with the rocks in the plastic bags, proved to be negligible when compared with that of the periphyton, no correction for this factor was necessary. All pigments of the periphyton collected from depths of ten through thirty-five feet decreased considerably during the sampling period; this trend was not shown by samples taken at depths of 2.5 and five feet. From Table II and Figure 3, it can be seen that chlorophyll *a* was the predominant pigment in nearly all samples. The minimum mean concentration was 0.190 milligrams per 100 square centimeters of rock surface at a depth of 2.5 feet, while the maximum mean concentration reached 0.510 milligrams per 100 square centimeters at a depth of thirty-five feet. Chlorophyll *c* and non-astacin carotenoids were present in somewhat lower concentrations, attaining minima at the same depth and maxima at different depths (see Figure 3). The minimum mean chlorophyll *c* concentration, 0.068 MSPU per 100 square centimeters, appeared at a depth of 2.5 feet and the maximum, 0.340 MSPU per 100 square centimeters, at a depth of thirty-five feet. The lowest mean concentration of non-astacin carotenoids was encountered at 2.5 feet (0.132 MSPU/100 cm^2) and the highest at twenty feet (0.311 MSPU/100 cm^2).

The observed ratio of chlorophyll *a* : chlorophyll *c* : non-astacin carotenoids, approximately 5:3:3, is to be expected because of the overwhelming preponderance of diatoms in the samples. According to Fox *et al.* (1967), six genera, *Achnanthes*, *Synedra*, *Cymbella*, *Navicula*, *Cocconeis*, and *Gomphonema*, accounted for over ninety per cent of the organisms in samples from all depths. The ratio of chlorophyll *c*/chlorophyll *a* at the 2.5-foot depth was 0.35; at five feet, 1.10; at ten feet, 0.61; at fifteen feet, 0.51; at twenty feet, 0.64; and at thirty-five feet, 0.67. No trend is apparent. The ratio of non-astacin carotenoids/chlorophyll *a* was more constant with depth. At a depth of 2.5 feet, the ratio was 0.67; at five feet, 0.76; at ten feet, 0.73; at fifteen feet, 0.74; at twenty feet, 0.63; and at thirty-five feet, 0.58. The ratio seems to decrease slightly as depth increases. The sampling period was not long enough to indicate any seasonal trends as far as the pigment ratios are concerned.

Chlorophyll *b* and astacin carotenoids were present in smaller amounts. Chlorophyll *b* reached a minimum of 0.036 milligrams per 100 square centimeters at a depth of 2.5 feet and a maximum of 0.158 milligrams per 100 square centimeters at a depth of ten feet; the minimum astacin carotenoid value, 0.015 MSPU per 100 square centimeters, appeared at 2.5 feet and the maximum, 0.061 MSPU per 100 square centimeters, at thirty-five feet. The chlorophyll *b* peak corresponds to a drop in chlorophyll *c* concentration (Figure 3), possibly indicating the presence of a relatively higher number of

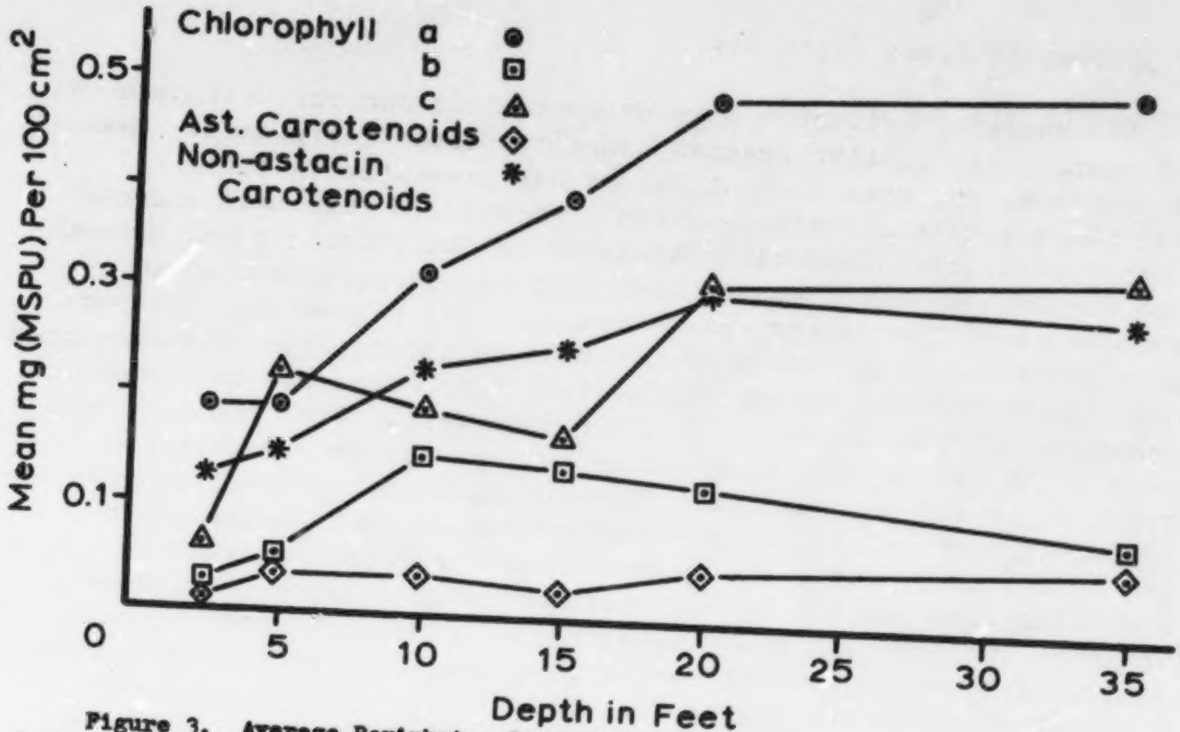

Figure 3. Average Periphyton Pigment Concentrations (per unit area of rock surface) at Standard Sampling Depths, Stony Point Bay, Lake Superior, 1966.

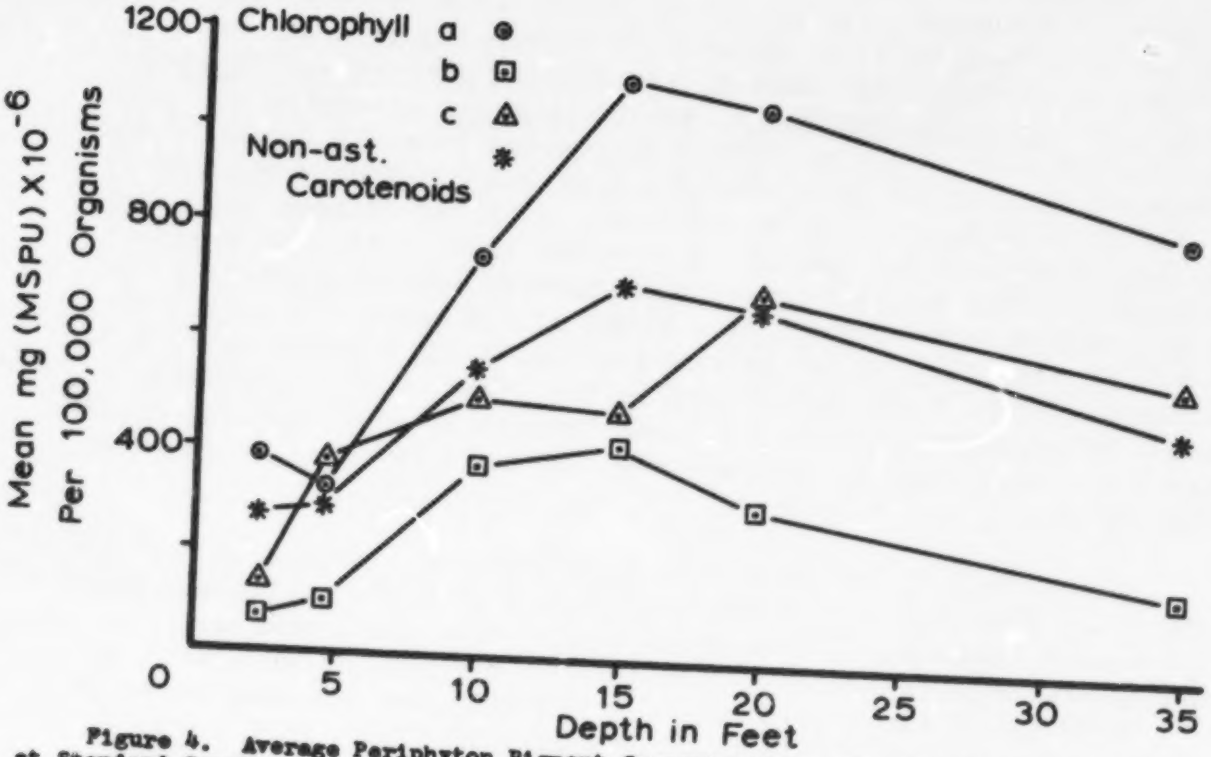

Figure 4. Average Periphyton Pigment Concentrations (per 100,000 Organisms) at Standard Sampling Depths, Stony Point Bay, Lake Superior, 1966.

TABLE II

PIGMENT CONCENTRATIONS OF NATURALLY OCCURRING PERIPHYTON FROM STANDARD DEPTHS, STONY POINT BAY, LAKE SUPERIOR, 1966. MILLIGRAMS OR MSPU PER 100 CM^2 ROCK SURFACE

	Depth in feet					
	2.5	5	10	15	20	35
Chlorophyll *a*						
Max.	0.232	0.275	0.729	0.803	1.399	0.969
Min.	0.125	0.120	0.136	0.096	0.139	0.277
Mean	0.191	0.198	0.328	0.338	0.491	0.510
Chlorophyll *b*						
Max.	0.054	0.094	0.430	0.421	0.450	0.304
Min.	0.012	0.001	0.010	0.015	0.017	0.001
Mean	0.040	0.058	0.158	0.149	0.134	0.090
Chlorophyll *c*						
Max.	0.091	0.517	0.733	0.404	0.778	1.060
Min.	0.027	0.010	0.010	0.011	0.091	0.103
Mean	0.066	0.197	0.199	0.171	0.316	0.340
Non-astacin carotenoids						
Max.	0.152	0.211	0.530	0.520	0.860	0.595
Min.	0.110	0.089	0.091	0.090	0.088	0.152
Mean	0.130	0.153	0.237	0.255	0.312	0.297
Astacin carotenoids						
Max.	0.027	0.096	0.143	0.076	0.130	0.183
Min.	0.001	0.001	0.010	0.008	0.017	0.020
Mean	0.015	0.044	0.046	0.032	0.053	0.061

TABLE III

CHLOROPHYLL CONTENT OF STONY POINT BAY PERIPHYTON (1966) AND OTHER COMMUNITIES ON A UNIT AREA BASIS

Investigator	Ecosystem	Chlorophyll (G/M^2)
	Stony Point Bay Periphyton	
	2.5'	.0297
	5'	.0453
	10'	.0685
	15'	.0658
	20'	.0941
	35'	.0940
	Average	.0660
Riley (1956)	Long Island Sound phytoplankton	0.1 - 0.6
Odum and Odum (1955)	Coral reef	0.5
Ichimura (1954)	Japanese lake	0.006
McConnell and Sigler (1959)	Rocky stream	0.05 - 1.0

periphytic green algae at depths of ten and fifteen feet than at other depths. This hypothesis was not borne out by the routine microscopic examination, as little difference was seen in the numbers of green algae at the various depths; however, it is possible that with the use of a random field counting method and a 200X magnification, some small green algae might be missed in a heavy sample. After careful re-examination of several samples, it was concluded that the reported percentage of green algae was, in fact, low.

The minute but persistent astacin carotenoid values observed may be attributable to the presence of animal grazers in the samples. Little difference can be seen in the concentrations at various depths; the minimum and maximum concentrations during the sampling period correspond in general with those of the other pigment groups. Part of the apparent astacin carotenoid value may be the result of an error in the formulas of Richards and Thompson (1952). This possible error (suggested by Parsons and Strickland, 1963) is due to the production of a positive animal carotenoid value by the plant xanthophyll, fucoxanthin.

Further inspection of Figure 3 reveals that all of the periphyton pigments tend to increase on a unit area basis from the shallow to the deeper parts of the bay. However, this increase is not due to a proportional rise in numbers of organisms with depth (see Figure 4); although peaks occur at fifteen or twenty feet, it will be seen that when the amount of each pigment per 100,000 organisms is plotted against depth, the same general increase in concentration occurs with depth. Therefore, higher pigment concentrations in the individual organisms were found to correspond directly to decreasing light intensity. The peaks observed at fifteen or twenty feet could be explained on the basis that larger aliquots were used to compensate for a relative scarcity of organisms present on the rocks from these depths. Such aliquots, when fine colloidal clay is present, may lead to slightly increased absorption readings, as centrifugation of the colloidal clay is difficult. If an adjustment is made for this factor, the amount of pigment per organism when plotted against increasing depth will approximate a sigmoid curve which reaches an asymptote at fifteen or twenty feet. It was assumed that the higher pigment concentrations in deeper water were a result of conditioning to a lower light intensity. This "sun and shade" reaction has been reported on several occasions as a phenomenon occurring in phytoplankton populations (Kozminski, 1938; Burkholder and Sieburth, 1961); however, the conditioning is much more apparent in the Stony Point Bay periphyton, because organisms attached at one depth must remain at that depth unless broken loose by violent currents, and are not continually mixed as phytoplankton organisms are. Thus the periphyton growing at a certain depth has a greater opportunity to adjust to light intensity than does the phytoplankton.

In order to compare the results of chlorophyll analyses performed with a broad spectrum instrument with those based on readings from a narrow-band spectrophotometer, the observed chlorophyll a, b and c concentrations (DK-2A) were added together and plotted against depth along with the Klett-Summerson total chlorophyll concentration values (Figure 5). The chlorophyll results based on readings with the Klett-Summerson colorimeter were considerably lower than the corresponding total chlorophyll concentrations obtained with the DK-2A method. This discrepancy may be due to the fact that the Klett #66 filter allows the passage of light only in the 640 to 700 millimicron range, thus effecting no measurement of chlorophyll _c_, which does not absorb visible light of wavelength greater than 635 millimicrons. Therefore, these observations do not lend support to the contention by Parsons and Strickland (1963) that Richards' formulas yield chlorophyll values which are too high. The data from the six standard sampling depths show that the narrow-band instrument produced total chlorophyll figures which averaged 1.7 times as high as those from the broad spectrum instrument. This factor, when calculated on the basis of data from each depth, varied from 1.49 to 1.90. It is interesting to note that the two methods agreed best on samples from 2.5 and fifteen feet, where the amounts of chlorophyll _c_ were lowest in relation to the other pigments.

Many investigators have reported chlorophyll concentrations on a unit area basis as a reflection of the general magnitude of biomass. In order to compare the data for Stony Point Bay with those reported for certain other ecosystems, the total chlorophyll values obtained by the DK-2A method were converted to grams per square meter (see Table III). These values ranged from 0.0297 at the 2.5-foot depth to 0.0941 at the twenty-foot depth. The average for the entire bay was 0.0660. Table III includes values calculated for some ecosystems studied by other workers. Those figures range from 0.006 grams of chlorophyll per square meter in a Japanese lake (Ichimura, 1954) to 0.6 grams per square meter, the upper limit reported for the phytoplankton of Long Island Sound by Riley (1956). The mean concentration for Stony Point Bay (0.0660) fits nicely within the range calculated for a rocky stream in Utah (McConnell and Sigler, 1959). It should be noted that since the reported concentrations for Stony Point Bay are based on the surface area of rocks which protrude above the bay floor, these figures cannot be compared directly with concentrations based on a unit area of water surface. The total surface area of the rocks in Stony Point Bay is greater than the area of the water surface above. Therefore, in directly comparing chlorophyll concentrations of phytoplankton with those of the periphyton within a given region, an allowance must be made for this factor.

Photosynthetic rate as measured by the Gilson respirometer was shown to be lowest for samples taken from a depth of 2.5 feet (39 microliters of oxygen evolved per square centimeter of rock surface per hour) and highest for samples from five feet (85 microliters of oxygen evolved per square centimeter per hour). Values obtained from samples taken from ten, fifteen, twenty, and thirty-five foot depths fell consistently between fifty and sixty microliters of oxygen evolved per square centimeter per hour (see Figure 6). These values represent _gross_ photosynthetic rate at 20° centigrade

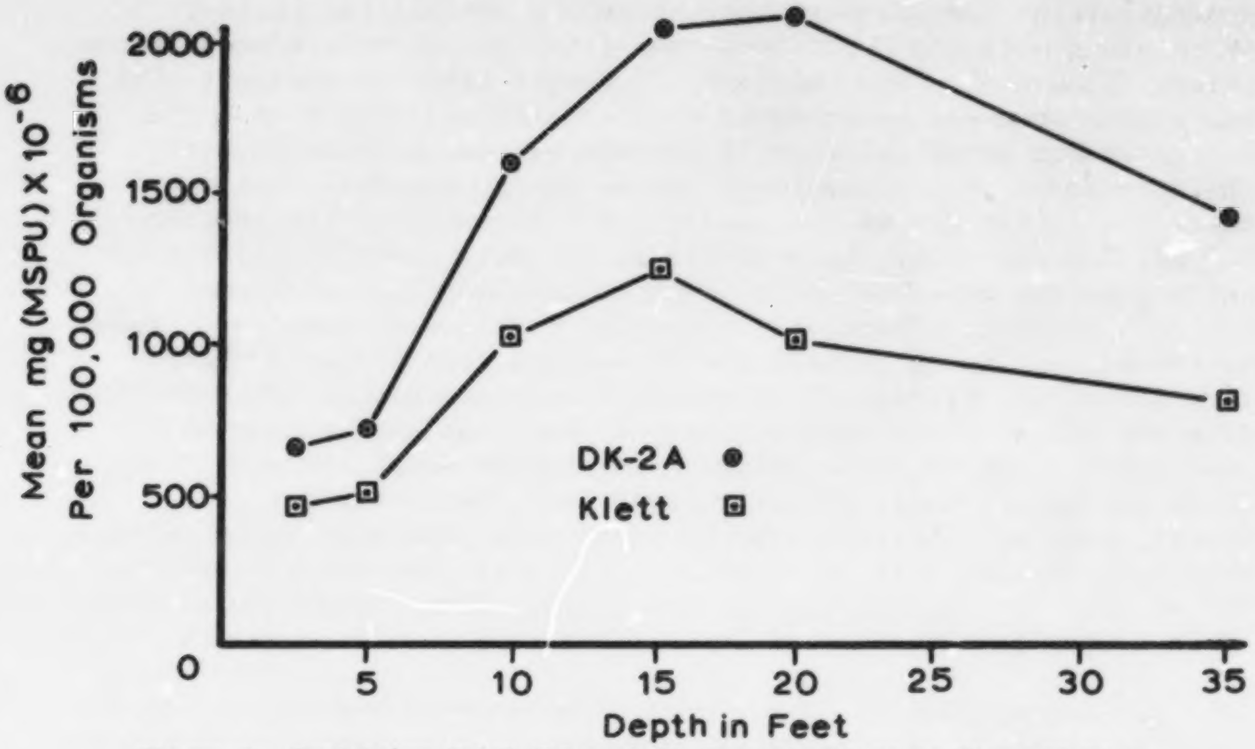

Figure 5. Periphyton Total Chlorophyll Concentrations as Measured by a Broad-Spectrum Colorimetric Method, and by a Narrow-Band Spectrophotometric Method.

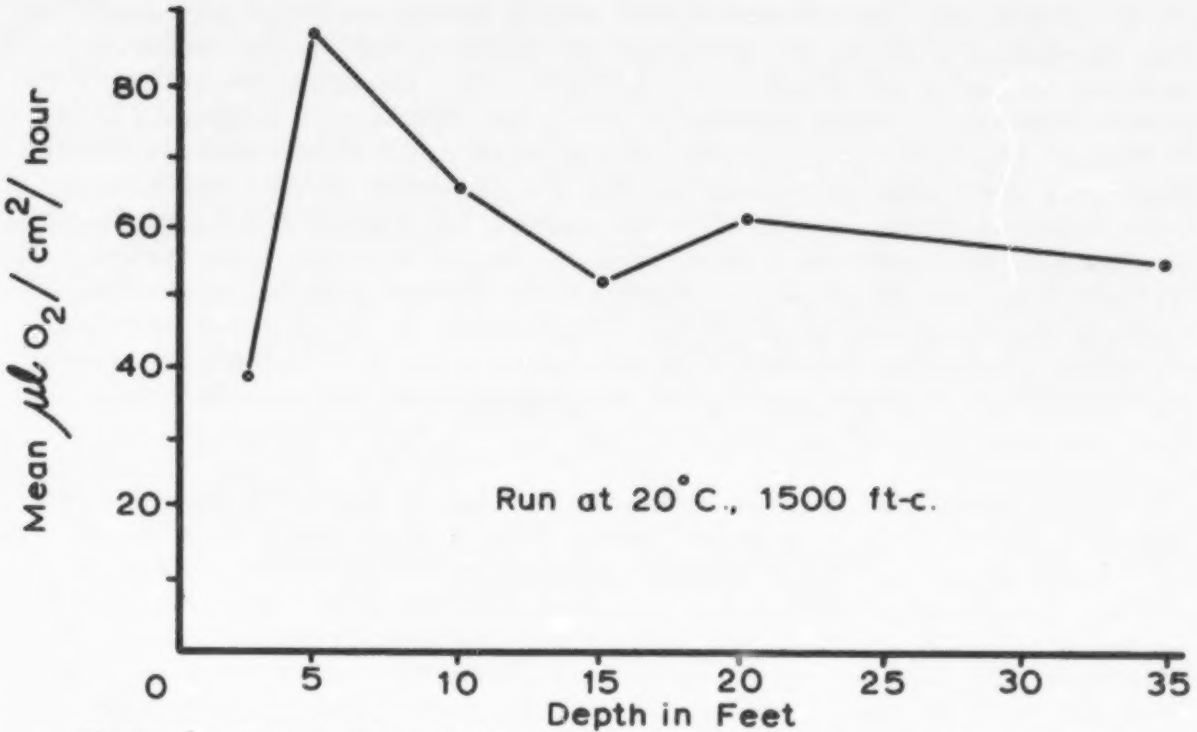

Figure 6. Average Gross Photosynthetic Rates (per unit area) for Samples from Standard Depths, Stony Point Bay, Lake Superior, 1966; Run at 20°C., 1500 Foot-Candles.

and a light intensity of 1500 foot-candles, and do not account for losses due to respiration. The mean value for the five-foot depth was influenced greatly by a single very high reading on one sampling day and is probably higher than the true average for the sampling period. This probable error is borne out by the photosynthesis/respiration ratios (Table IV). The ratio for the five-foot sample (4.40) is inconsistent with the values calculated for samples from the other depths (3.03 to 3.43).[5] The overall mean P/R ratio for Stony Point Bay periphyton under the test conditions was found to be 3.39. Published data relating the photosynthetic and respiration rates of periphyton are rare. However, a striking comparison may be made between the average P/R ratio for Stony Point Bay periphyton (3.39) and that calculated from the data of Jackson (1966) for _Cladophora fracta_ in Lake Ontario (3.42). Riley's (1957) data for the algae of the Sargasso Sea yield a P/R value of 3.06. A value of 2.91 has been calculated for the photosynthetic organisms of Silver Springs, Florida (Odum, 1957).

Since the P/R ratios for samples from all depths in Stony Point Bay are similar except for the five-foot samples, the net photosynthetic rates follow nearly the same pattern as the gross rates (Table IV). The net rates ranged from 27.5 microliters of oxygen evolved per square centimeter of rock surface per hour for the samples from 2.5 feet to 67.9 microliters of oxygen per square centimeter per hour for the five-foot samples. Values for the remaining depths varied between 35.9 and 45.3. The overall mean rate for net photosynthesis in samples from all depths was 43.3 microliters of oxygen evolved per square centimeter per hour.

Assuming fifteen hours of daylight per day, the photosynthetic rates were converted to production rates in terms of carbon fixed (Table IV). Net production varied between 1.62 grams of carbon fixed per square meter per day at a depth of 2.5 feet and 4.49 grams of carbon fixed per square meter of rock surface per day at five feet; the average value for all sampling stations was 2.63 grams of carbon fixed per square meter per day. These values take into account losses due to daytime and nighttime respiration, and represent true net production figures under the test conditions. The figures were again converted to reflect net production in terms of organic matter. For purposes of calculation, it was assumed that all carbon was fixed in the form of glucose (see Table IV). Thus the production rates ranged from 4.05 grams production (as glucose) per square meter per day to 11.22 grams per square meter per day; the average rate for samples from all depths was 6.58 grams (as glucose) per square meter per day. Again, these values are corrected for respiration losses and are net production rates for the test conditions (20° C., 1500 foot-candles).

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[5] The 1967 data subsequently showed that no significant peak occurs at five feet. The P/R ratio for the five foot samples during that year was 3.46, while the ratio for the other depths ranged from 2.96 to 3.36.

TABLE IV

PHOTOSYNTHESIS DATA FOR PERIPHYTON SAMPLED AT DIFFERENT DEPTHS, STONY POINT BAY, 1966; RUN AT 20°C, 1500 FOOT-CANDLES

	Sampling depth in feet						
	2.5	5	10	15	20	35	Mean
Gross photosynthesis ul O_2/cm^2/hr	+39.7	+87.9	+66.3	+53.6	+61.5	+55.6	+60.7
Respiration ul O_2/cm^2/hr	-12.2	-20.0	-21.0	-17.7	-17.9	-16.0	-17.3
Net photosynthesis ul O_2/cm^2/hr	+27.5	+67.9	+45.3	+35.9	+43.6	+39.6	+43.4
P/R	3.26	4.40	3.14	3.03	3.43	3.10	3.39
Net production							
Grams carbon fixed per M^2 per day	1.62	4.49	2.63	2.03	2.64	2.41	2.63
Grams (as glucose) per M^2 per day	4.05	11.22	6.57	5.07	6.60	6.02	6.58

TABLE V

PERIPHYTON VOLUMES AND DRY WEIGHTS AT THE STANDARD DEPTHS, STONY POINT BAY, LAKE SUPERIOR, 1966

		Depth in feet					
		2.5	5	10	15	20	35
Dry weight (Mg. per cm^2 rock surface)	Max.	10.0	15.1	19.7	30.0	32.0	24.3
	Min.	2.5	3.1	5.1	6.0	2.1	5.3
	Mean	6.5	7.1	10.7	14.0	13.4	11.6
Volume (Ml. per 100 cm^2)	Max.	3.35	2.98	9.27	8.55	4.89	6.74
	Min.	2.62	2.20	2.29	1.72	2.80	1.85
	Mean	3.00	2.56	4.05	3.71	3.36	3.98

An interesting relationship between oxygen yield, chlorophyll concentration and sampling depth is suggested by Figure 7. The volume of oxygen evolved per milligram of total chlorophyll begins at 13.5 x 10^3 microliters per hour at 2.5 feet, rises to 22.3 x 10^3 microliters per hour at five feet, and then falls off asymptotically through the remaining depths. If the five-foot value is ignored (this figure is probably too high), a smooth, slowly descending curve is produced. If photosynthetic rate increases proportionately with increased pigment concentration, then the oxygen : pigment ratio should approximate a constant value in all samples, regardless of their source, when the samples are exposed to excess light. However, recalling that pigment concentrations were shown to increase with depth, and noting from Figure 7 that the oxygen : pigment ratio is not constant for organisms taken from different depths, one may assume that once a certain low light level is reached, the further addition of pigments by an algal cell in decreased light will not necessarily maintain the expected photosynthetic rate. Apparently, conditioning to a certain light intensity affects the photosynthetic capacity of a pigment unit as well as influencing pigment concentrations. This factor is important in the consideration of the effects of short-term and long-term increases in turbidity on periphyton productivity, whether such turbidity is caused by natural runoff from the land or by advancing water pollution.

The photosynthesis and chlorophyll data from Figure 7 were also calculated as grams of carbon fixed per gram of chlorophyll so that comparisons of these "assimilation numbers" could be made with those reported elsewhere for other communities. The assimilation value determined for Stony Point Bay at a depth of 2.5 feet was 7.2 grams of carbon fixed per hour per gram of chlorophyll; at five feet, 11.9; at ten feet, 4.8; at fifteen feet, 3.7; at twenty feet and thirty-five feet, 3.2. The average of these figures is 5.7 grams of carbon fixed per hour per gram of chlorophyll. Discarding the five-foot value, which is probably in error as previously explained, the average becomes 4.4. This figure compares quite well with the 3.7 reported by Ryther and Yentsch (1957) for marine phytoplankton. It is, however, considerably higher than assimilation numbers calculated for various ecosystems by certain other workers. For example, Ichimura (1954) reported 2.36 grams of carbon fixed per hour per gram of chlorophyll in Lake Suwa, Japan. Odum and Odum (1955) found the value for a coral reef to be 1.5, while the data of McConnell and Sigler (1959) show 0.75 grams of carbon fixed per hour per gram of chlorophyll in a rocky stream in Utah.

The dry weights of the 1966 periphyton samples are presented in Table V. The average weights correlate rather well with the pigment concentrations, but this relationship may be purely coincidental. Since the relationship between pigment concentrations and numbers of organisms has been shown to depend on the depth from which the sample was taken, there is reason to believe that the amount of pigment per unit of dry weight would also vary from one depth to another. The mean dry weight was lowest at the 2.5-foot depth

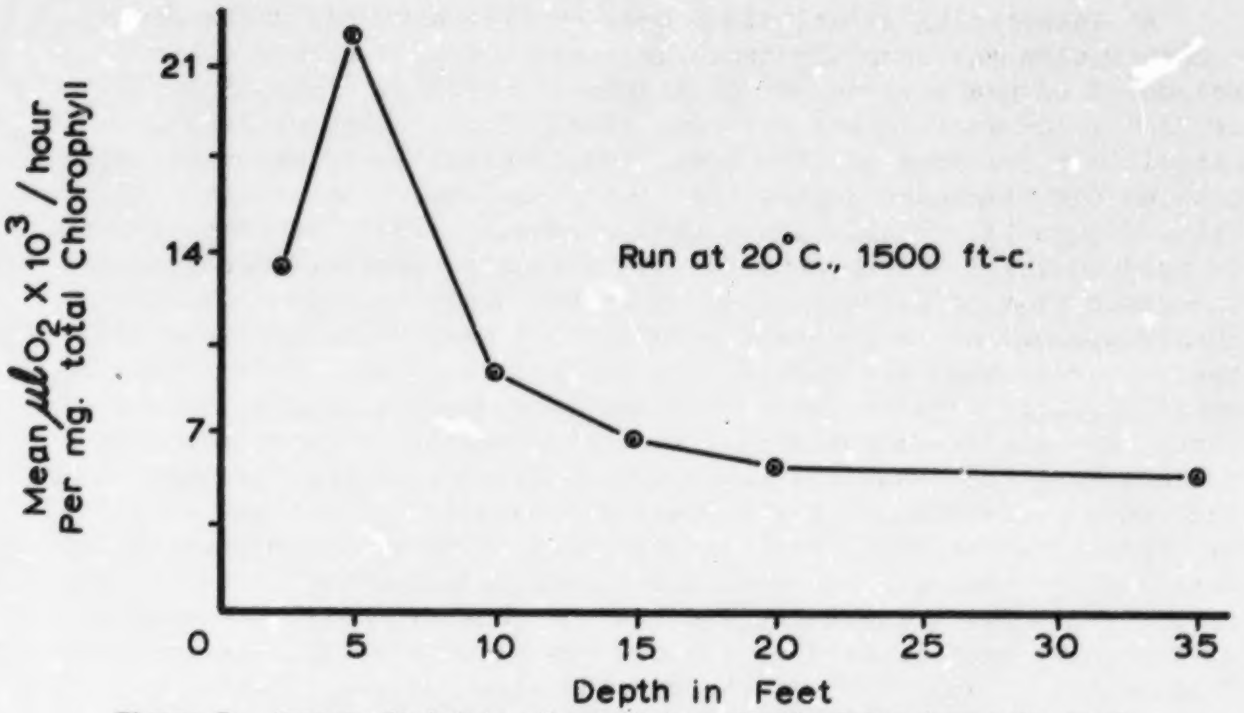

Figure 7. Average Periphyton Gross Photosynthetic Rates (per unit total chlorophyll) at Standard Sampling Depths, Stony Point Bay, Lake Superior, 1966.

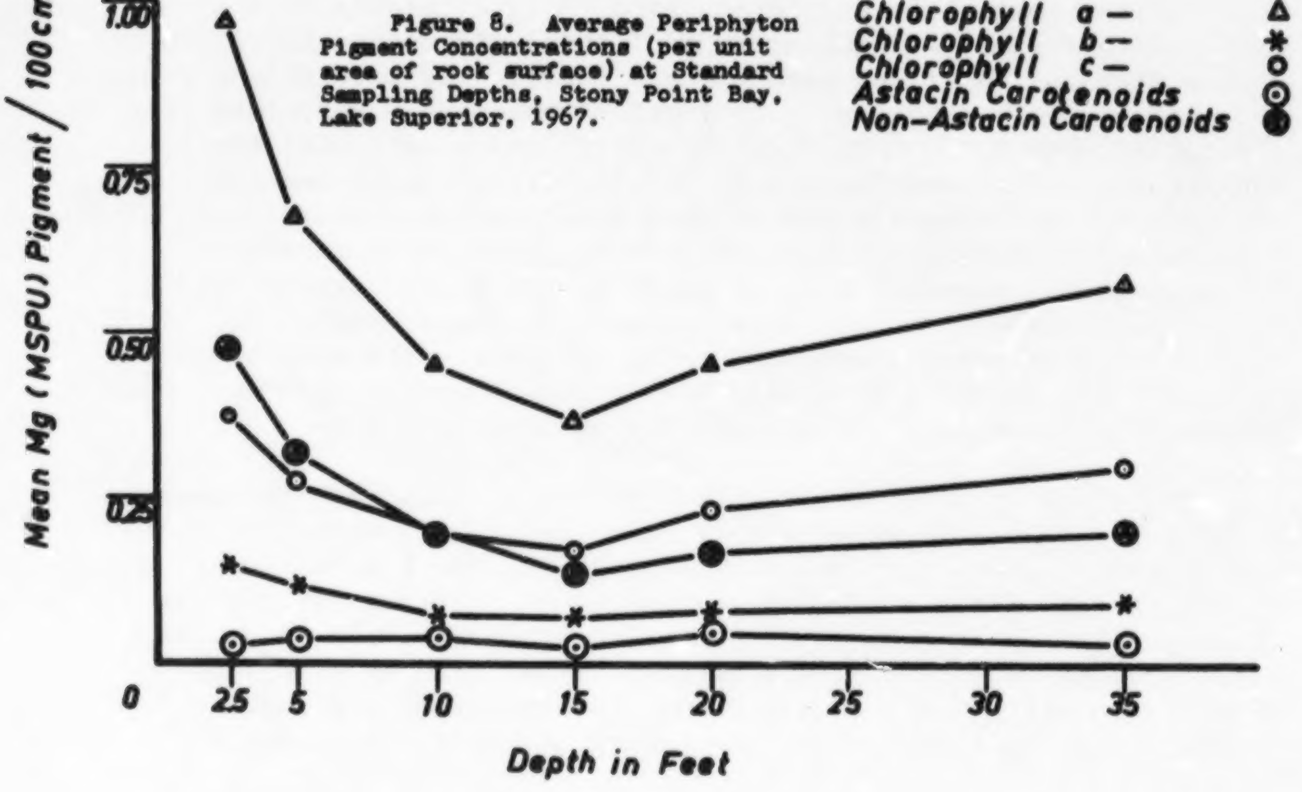

Figure 8. Average Periphyton Pigment Concentrations (per unit area of rock surface) at Standard Sampling Depths, Stony Point Bay, Lake Superior, 1967.

(6.5 milligrams per square centimeter of rock surface) and highest at the fifteen-foot depth (14.0 milligrams per square centimeter). The total number of organisms was lowest at fifteen feet (Fox et al., 1967). The weight of the periphyton was less at thirty-five feet than at the intermediate depths. This pattern can be explained on the basis that the organisms near shore are sometimes removed from the rocks by wave action while the organisms in the deeper areas are not affected. The lower biomass at thirty-five feet is probably due to relatively low light intensity and temperature. Varying amounts of sand and silt accompanied the organisms in the samples; apparently, a larger proportion of sand and silt was present in the samples from the fifteen-foot depth than those from other depths. This point was borne out by visual examination of the samples. On the basis of the 1966 mean dry weights for all depths, the standing crop of periphyton in Stony Point Bay was calculated to be 104 grams per square meter or 37.1 tons for the entire bay.

The volumes of the settled periphyton samples are also shown in Table V. The mean values range from 3.00 milliliters of periphyton per 100 square centimeters of rock surface at the five-foot depth to 4.05 milliliters per 100 square centimeters at the ten-foot depth. These results compare reasonably well with the dry weights, inasmuch as the volume determinations were also subject to the influence of sand and silt in the samples. Dry weight and volume determinations would appear to be useful in the estimation of the general magnitude of biomass in the periphyton community.

Enough quantitative data were gathered during the summer of 1966 to allow the formulation of certain tentative conclusions regarding the biomass of Stony Point Bay periphyton and the relationships between the various parameters which were observed. The periphyton pigments were dominated by chlorophyll a, with chlorophyll c and non-astacin carotenoids approximately equal as secondary pigments. Low chlorophyll b concentrations indicate the presence of a relatively low proportion of green algae to diatoms. It is apparent that the organisms increased their pigment concentrations in deeper water, probably in response to lower light intensity. Chlorophyll per square meter and carbon fixed per square meter were shown to be of the same order of magnitude as for other ecosystems. Astacin carotenoid values, while quite low, probably reflect the association of certain animal forms with the periphytic algae. The data indicate that any single measurement, such as pigment analysis, enumeration of organisms, or the determination of weight, volume or photosynthetic rate, will probably not show the true productivity of the periphyton.

It was deemed necessary to confirm the 1966 results by obtaining more data on the same bay with similar techniques. In addition, the 1966 data raised a number of questions which could be answered only by a more extensive sampling program. Among these questions were the following: Are periphyton pigment concentrations actually so variable with depth as indicated by the 1966 data? Are there seasonal changes in concentration on an area basis, and do consistent differences in pigment ratios occur with depth? What is the relationship between organic weight, total dry weight and other parameters of biomass? Would further sampling confirm the apparent decrease in efficiency of the pigment unit as the pigments become more concentrated?

III. 1967 FINDINGS

The experience gained in sampling and analysis of periphyton in 1966, when added to the information obtained on the various aspects of periphyton ecology, made a much more comprehensive investigation possible in 1967. The weather, too, during the summer of 1967, was very favorable and the sampling program was not seriously interrupted by storms. For this reason, greater emphasis should be given to the data obtained during that year. For greater clarity and effectiveness, this chapter has been divided into three parts, each dealing with a separate approach to the investigation of Lake Superior periphyton. The first section is concerned with the naturally occurring periphyton of Stony Point Bay, and the second with the regrowth study conducted in the same bay, while the third section deals with an investigation of the periphyton communities of north shore areas other than Stony Point Bay.

Naturally Occurring Periphyton, Stony Point Bay

Routine samples of the periphyton were collected in Stony Point Bay from July 11 to September 15, 1967. An additional sampling trip was made on November 10. As in 1966, three rocks were taken from each standard depth (2.5, 5, 10, 15, 20 and 35 feet) during each sampling run. Sampling trips were made on seventeen days (twice each week) during which a total of 306 rocks was collected.

The pigment concentrations, on a unit area basis, for each depth are shown in Figure 8. Each point represents the average concentration of one pigment type at one depth during the entire sampling period. Chlorophyll a was the predominant pigment at all depths, ranging from a minimum mean concentration of 0.330 milligrams per 100 square centimeters of rock surface at a depth of fifteen feet to a maximum of 0.976 milligrams per 100 square centimeters at a depth of 2.5 feet. The mean concentration for samples from the thirty-five foot depth was 0.583 milligrams per 100 square centimeters. The same pattern was exhibited by the other plant pigment groups. The chlorophyll c concentration began at 0.386 MSPU per 100 square centimeters at a depth of 2.5 feet, fell to 0.163 MSPU per 100 square centimeters at fifteen feet, and then rose to 0.298 MSPU per 100 square centimeters at thirty-five feet. The non-astacin carotenoid values were similar in magnitude, varying from 0.475 MSPU per 100 square centimeters at the 2.5 foot depth to 0.132 MSPU per 100 square centimeters at fifteen feet. At the thirty-five foot depth, the mean concentration was 0.201 MSPU per 100 square centimeters. Chlorophyll b was present at all depths in considerably lower concentrations than the other plant pigments. The maximum chlorophyll b concentration appeared at a depth of 2.5 feet (0.146 milligrams per 100 square centimeters) while the minimum concentration occurred at fifteen feet (0.064 mg./100 cm^2). The concentration at the thirty-five foot depth was intermediate in magnitude (0.096 mg./100 cm^2). Astacin carotenoids were present in small amounts, but did not follow the pattern of concentration exhibited by plant pigments in terms of sampling depth. The highest mean concentration of astacin carotenoids was found in samples from a depth of thirty-five feet (0.035 MSPU/100 cm^2) and the lowest in samples from 2.5 feet (0.015 MSPU/100 cm^2).

The curves representing the relationships between periphyton concentrations on an area basis and sampling depth in 1967 (Figure 8) bear little resemblance to those of 1966 (Figure 3). Differences in both shape and magnitude are obvious; however, it will be noted that the major differences occur only at depths from 2.5 feet to ten feet. The mean chlorophyll a̲ concentration found at the 2.5 foot depth in 1967 (0.976 milligrams per 100 square centimeters) was more than five times as high as the corresponding figure for 1966 (0.191 mg./100 cm^2). The amounts of chlorophylls b̲ and c̲ and non-astacin carotenoids were four to five times higher at 2.5 feet in 1967 than in 1966. At the five foot depth, all plant pigment groups were two to three times higher in 1967. The mean chlorophyll a̲ concentration at the ten foot depth was thirty per cent higher in 1967 than in 1966, but the other plant pigment concentrations were not significantly different at that depth. At the remaining depths (15, 20 and 35 feet), chlorophylls a̲, b̲ and c̲, and non-astacin carotenoids occurred in approximately the same concentrations in 1967 as in 1966. Although the mean concentration of astacin carotenoids was low for both summers, the averages for 1966 were somewhat higher than those for 1967 at all depths except 2.5 feet, where the values were identical. The pigment concentration values of 1967 are considered to be more accurate than those obtained in 1966, because a correction was made for turbidity in the acetone-pigment solutions. This correction was accomplished by subtracting the absorbance reading at 750 millimicrons, a wavelength at which none of the pigments absorbs any light, from the absorbance values at 480, 510, 630, 645 and 665 millimicrons, before these readings are used for calculation of pigment concentrations.

As in 1966, the pigment concentrations calculated on an area basis do not directly reflect the amount of periphyton growth at each depth in the bay. This point is illustrated by the relationship between total chlorophyll and ash-free dry weight of periphyton at the standard depths (see Figure 9). The amount of total chlorophyll rose from 5.58×10^{-3} milligrams per milligram of ash-free dry weight at 2.5 feet to 8.14×10^{-3} milligrams per milligram of ash-free dry weight at thirty-five feet. The major increase in concentration occurred between the fifteen and twenty foot depths (6.12×10^{-3} mg. chlorophyll/mg. ash-free dry weight to 7.85×10^{-3} mg. chlorophyll/mg. ash-free dry weight). The relationship between chlorophyll concentration and biomass is further established by consideration of the total numbers of organisms at each depth. A continuous downward trend in the counts as depth increased was obvious. The organisms in deeper water apparently had increased their pigment concentrations in response to lower light intensity as in 1966. However, the relationship between total chlorophyll and ash-free dry weight (Figure 9) indicates that this increase was not so marked in 1967 as the pigment per

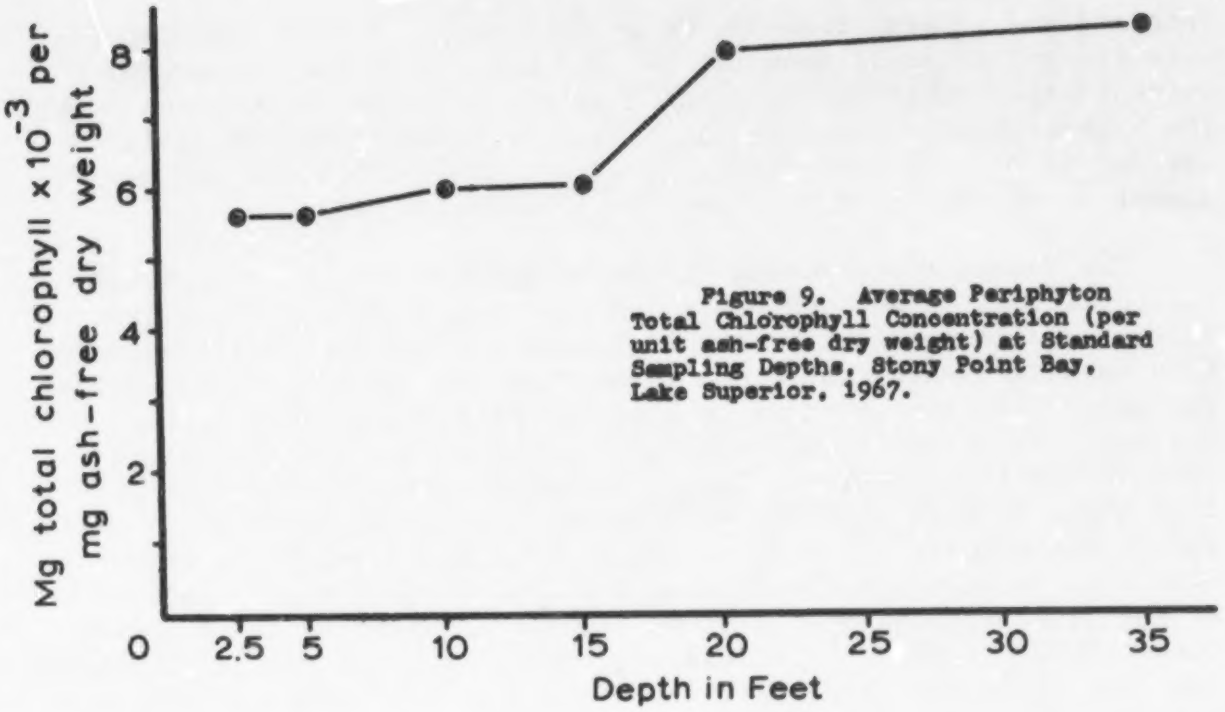

Figure 9. Average Periphyton Total Chlorophyll Concentration (per unit ash-free dry weight) at Standard Sampling Depths, Stony Point Bay, Lake Superior, 1967.

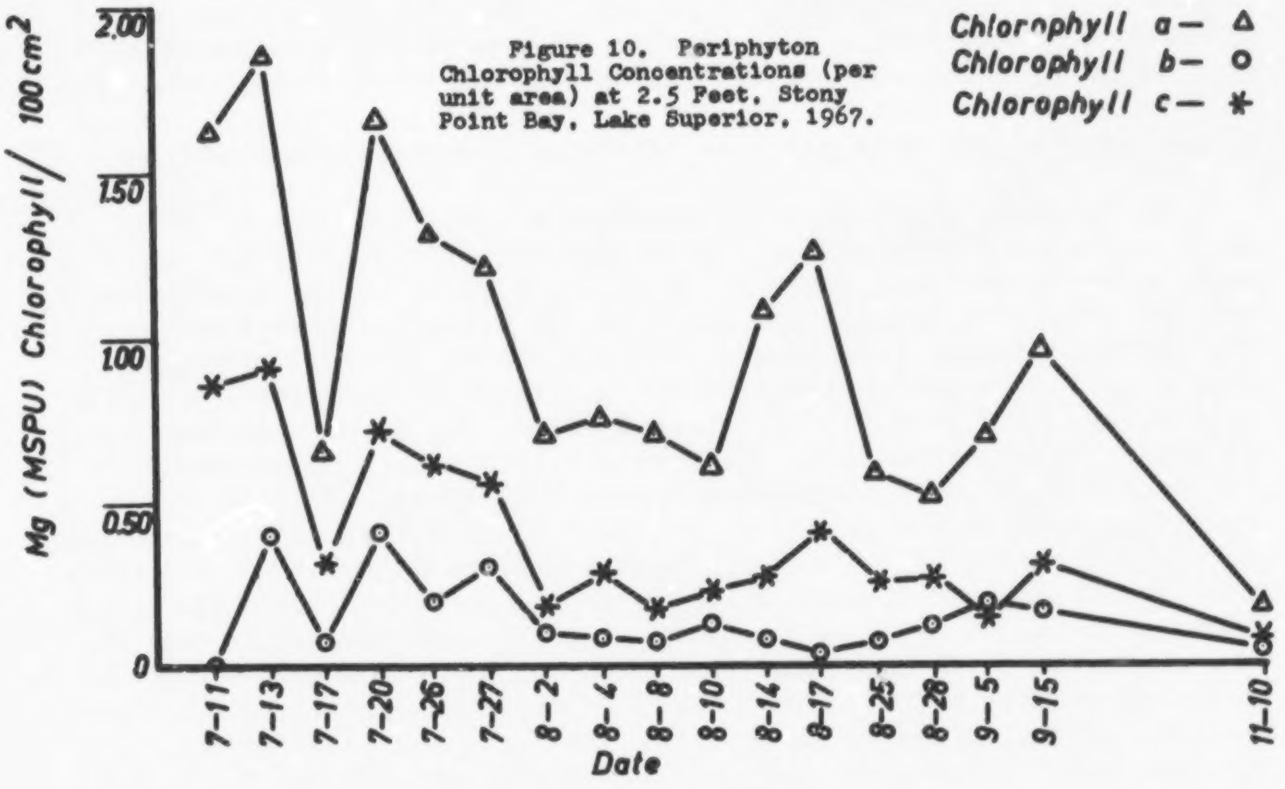

Figure 10. Periphyton Chlorophyll Concentrations (per unit area) at 2.5 Feet, Stony Point Bay, Lake Superior, 1967.

organism ratios of 1966 would suggest.

The increased periphyton biomass in the shallow water of Stony Point Bay in 1967 (indicated by pigment concentrations) may be explained on the basis of weather. Very few violent storms arose during the summer of 1967; the organisms growing in the shallow waters were disturbed much less often by currents and wave action than in 1966. East and northeast winds cause the most severe turbulence along the north shore of Lake Superior because their course parallels the long axis of the lake. United States Department of Commerce local climatological data show that no northeast winds occurred in the general area during the 1967 sampling period. East winds occurred on only eleven of the sixty-seven days, or sixteen per cent of the time. During the summer of 1966, east and northeast winds prevailed thirty-nine per cent of the time. These data reinforce personal observations which indicated that the waters of Stony Point Bay were much more calm during the 1967 season than in 1966. The hypothesis is that many periphytic organisms were washed away from the shallow areas in 1966, while those in relatively deep water were not affected by wave action. Thus the biomass in deep water was of approximately the same magnitude during both summers.

The variations in pigment concentrations at each depth (on a unit area basis) according to sampling date are presented in Figures 10 through 21. The points represent the individual measurements from which the average concentrations at each depth (Figure 8) were calculated. While the general pattern of Figure 8 may be seen by superimposing the individual graphs and observing the area under each curve, it is obvious that the variation in terms of time is not the same at each depth. In discussing these variations, the sample taken on November 10 will be considered separately.

At the 2.5 foot depth (Figures 10 and 11) the maximum concentrations of all five pigment groups occurred early in the season; all of the pigments peaked on July 13, except the astacin carotenoids, which were highest on the first sampling day (July 11). The minimum values for each pigment type at 2.5 feet were obtained near the end of August. The maximum concentrations were about three times as high as the minimum concentrations. For example, the maximum chlorophyll a value was 1.863 milligrams per 100 square centimeters on July 13, while the minimum was 0.547 milligrams per 100 square centimeters on August 28. While major peaks in the curves appeared on July 20, August 17 and September 15, the general downward trend of each of the pigment groups during the season is apparent.

There is no suggestion of a downward trend in pigment concentrations during the summer at the five foot depth (see Figures 12 and 13). The concentration of total pigments per unit area remained rather constant throughout the sampling period. The maximum concentration of chlorophyll a (0.930 mg./100 cm^2) and non-astacin carotenoids (0.465 MSPU/100 cm^2) occurred on July 27. Slightly lower peaks appeared on August 10 and 28. The concentrations of chlorophylls b, c, and astacin carotenoids reached their highest levels on August 28.

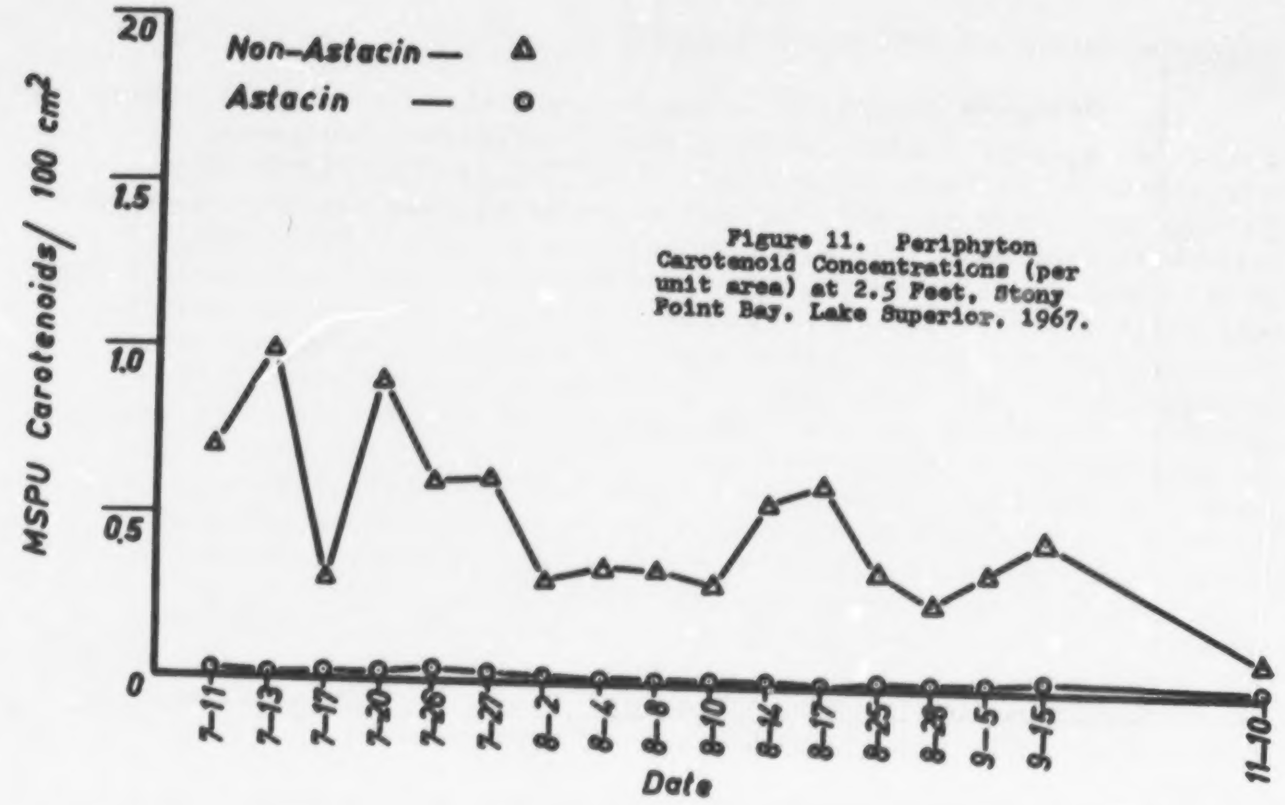

Figure 11. Periphyton Carotenoid Concentrations (per unit area) at 2.5 Feet, Stony Point Bay, Lake Superior, 1967.

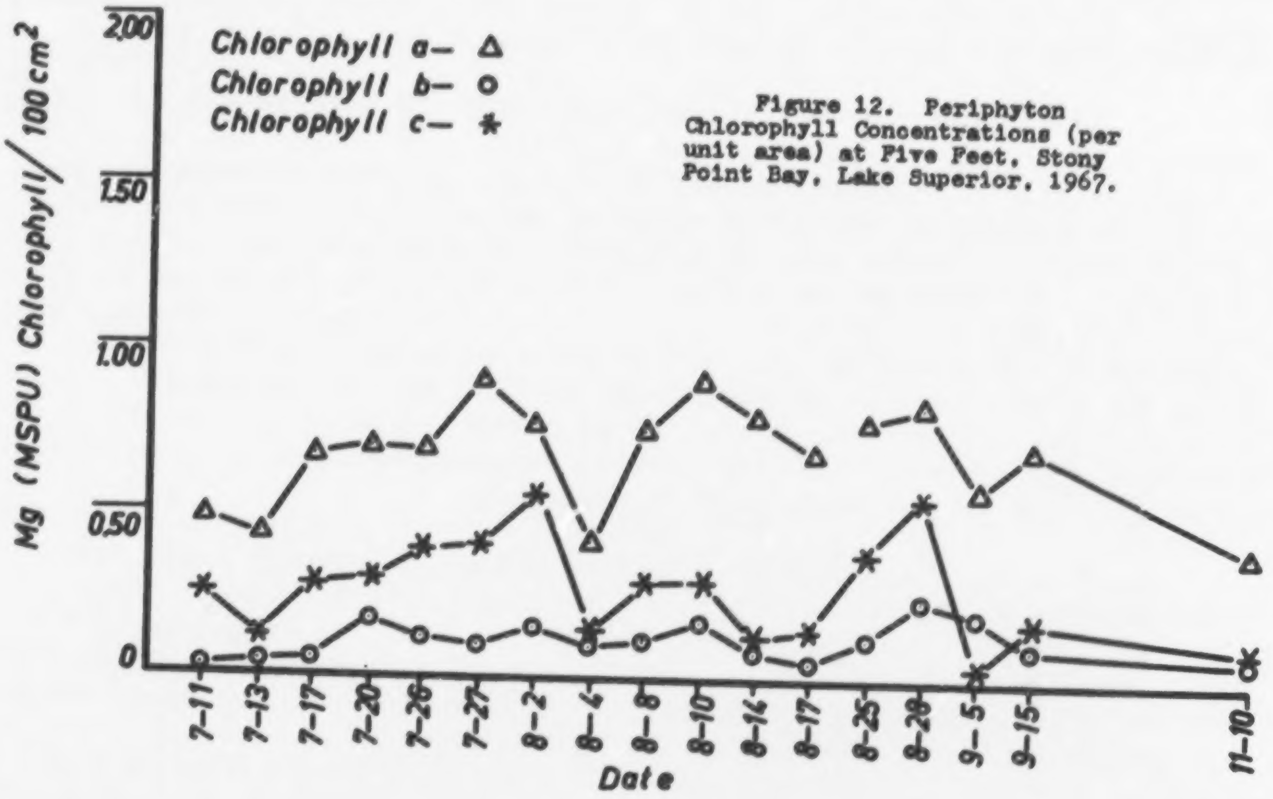

Figure 12. Periphyton Chlorophyll Concentrations (per unit area) at Five Feet, Stony Point Bay, Lake Superior, 1967.

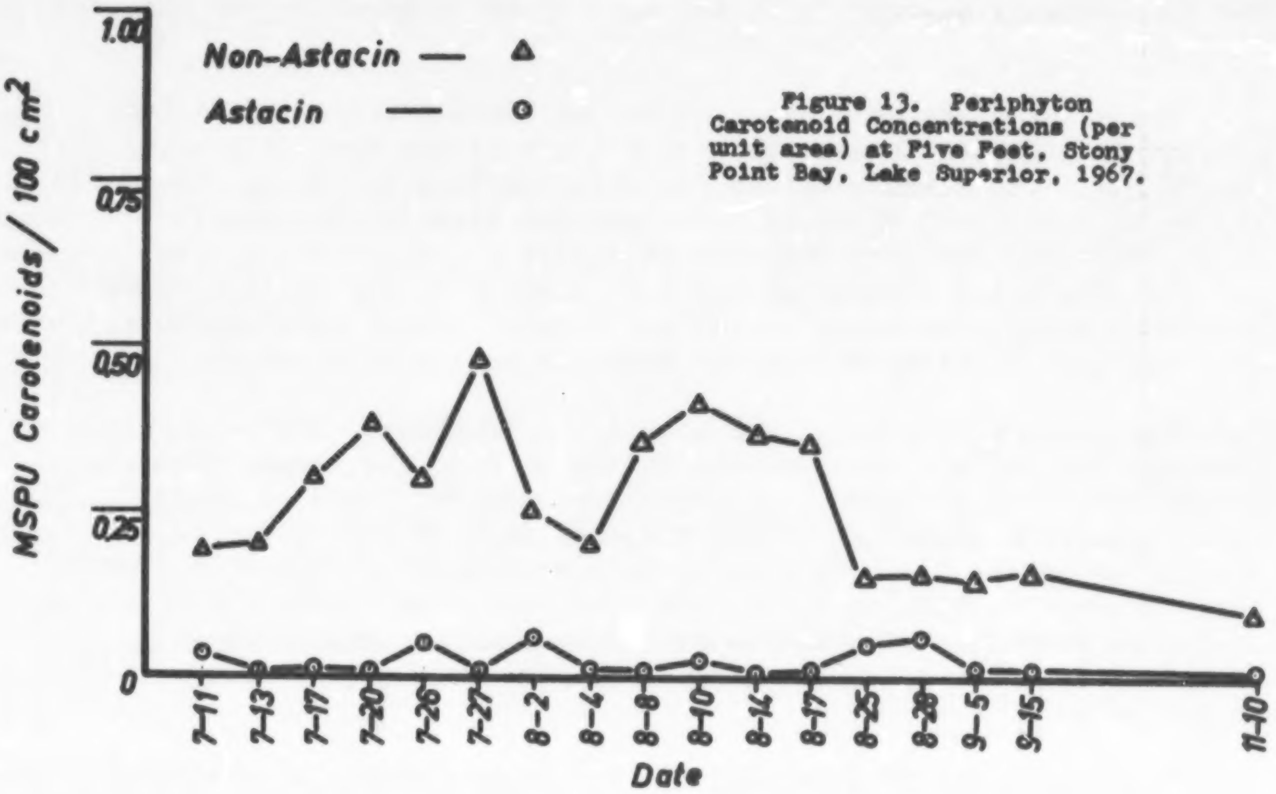

Figure 13. Periphyton Carotenoid Concentrations (per unit area) at Five Feet, Stony Point Bay, Lake Superior, 1967.

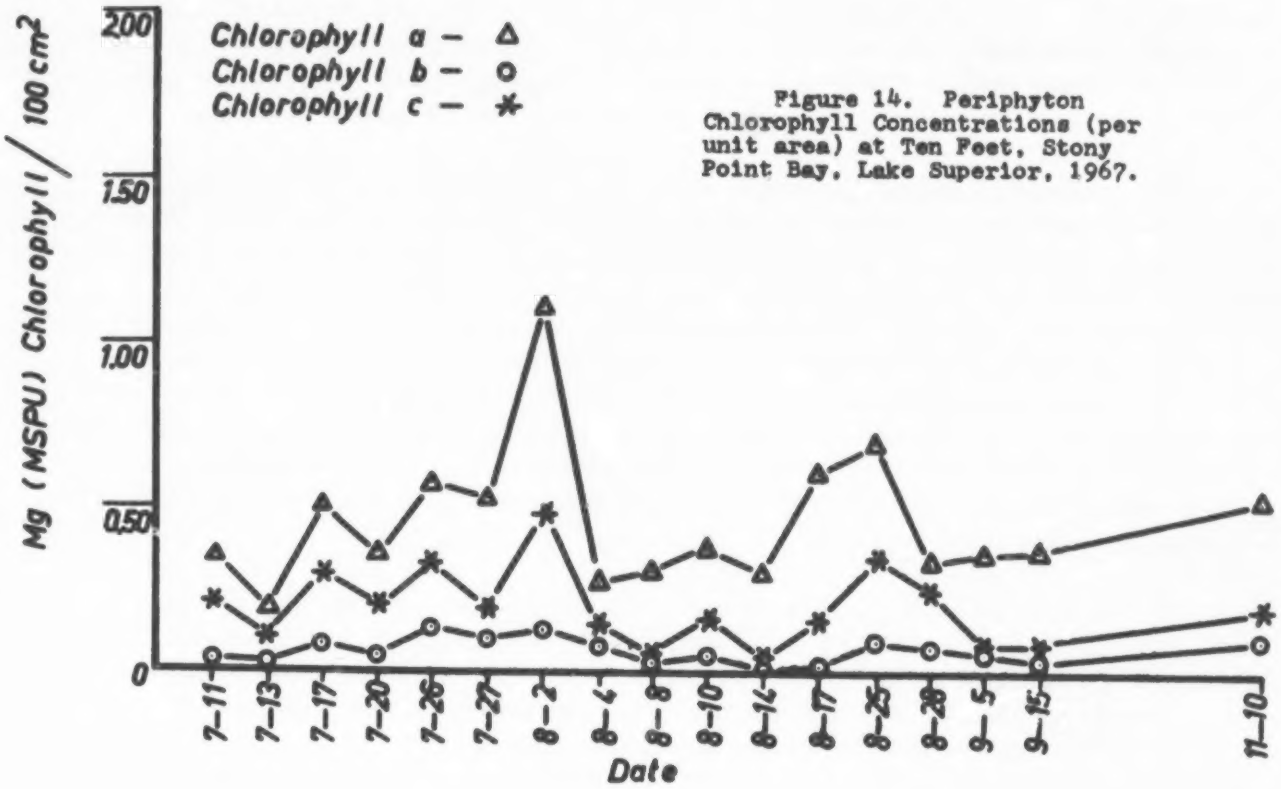

Figure 14. Periphyton Chlorophyll Concentrations (per unit area) at Ten Feet, Stony Point Bay, Lake Superior, 1967.

The most obvious depression in the major plant pigment curves occurred on August 4.

Two major peaks were observed in the concentrations of all the periphyton pigments in samples from a depth of ten feet (Figures 14 and 15). The maximum values for chlorophyll a (1.102 mg./100 cm^2), chlorophyll c (0.472 MSPU/100 cm^2), and non-astacin carotenoids (0.463 MSPU per 100 cm^2) occurred on August 2. Chlorophyll b and astacin carotenoid concentrations were highest on August 25. Between these two dates, the level of all the pigment groups remained quite low. No general trend during the sampling period is apparent.

The pigment concentrations at fifteen feet were lower and less variable than at all other depths during most of the summer (Figures 16 and 17). The chlorophyll a curve includes two peaks of nearly equal magnitude (0.468 mg. per 100 cm^2 on July 27, and 0.490 mg./ 100 cm^2 on August 17). The non-astacin carotenoid values show a very similar pattern, peaking on the same two days. Chlorophyll c, however, peaked on July 20, while chlorophyll b reached its maximum level on August 28. The concentrations of all the pigment types were lowest in September.

Figures 18 and 19 show that the periphyton pigments generally increased on a unit area basis at a depth of twenty feet during the sampling period. Chlorophyll a rose from 0.201 milligrams per 100 square centimeters on July 11 to a maximum of 0.784 milligrams per 100 square centimeters on August 25. In similar fashion, the non-astacin carotenoid level increased from 0.036 MSPU per 100 square centimeters on July 11 to 0.319 MSPU per 100 square centimeters on September 5. The maximum chlorophyll c value (0.473 MSPU/100 cm^2) appeared on August 25, as did the highest chlorophyll b level (0.142 mg./100 cm^2). The major pigments underwent a series of continuous increases and decreases between August 10 and September 15.

The pigment concentrations at thirty-five feet also exhibited a general increase during the summer (see Figures 20 and 21). The minimum chlorophyll a value, 0.303 milligrams per 100 square centimeters, occurred on July 17 and the maximum, 1.046 milligrams per 100 square centimeters, on September 5. Chlorophylls b, c, and non-astacin carotenoids reached their highest levels on September 5 or 15. The seasonal rise in the major pigment concentrations was generally smooth, the only apparent depression occurring on August 28. The astacin carotenoid values for the thirty-five foot samples, as for those from all other depths, remained very low and varied little during the sampling period.

It is not possible to account for each rise and fall in the pigment concentrations at the various depths throughout the summer. However, there are reasonable explanations for differences between the trends exhibited by the pigment concentrations at various depths, and for some decreases in concentration on specific days. The rather large variation in pigment concentrations at the shallower depths (2.5 to 10 feet) during the sampling period probably reflects the action of waves on the periphyton. The depressions and peaks rep-

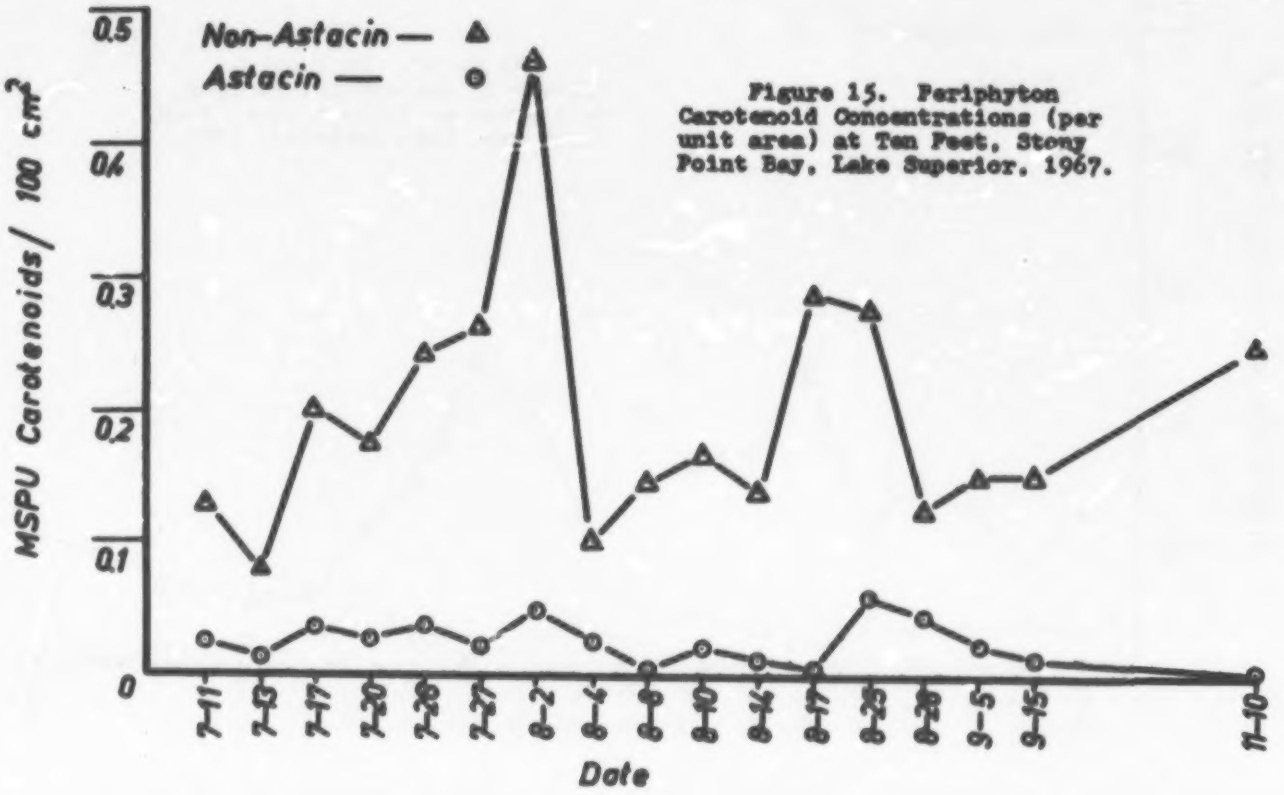

Figure 15. Periphyton Carotenoid Concentrations (per unit area) at Ten Feet, Stony Point Bay, Lake Superior, 1967.

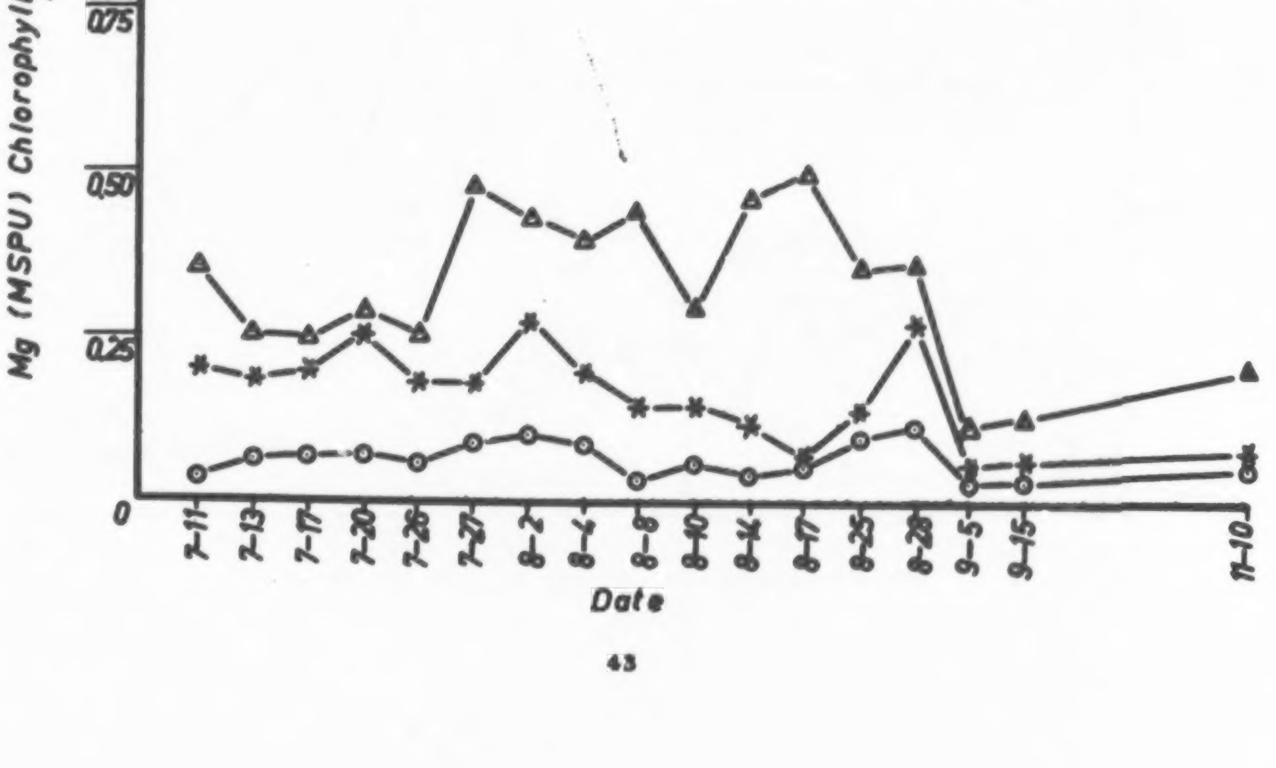

Figure 16. Periphyton Chlorophyll Concentrations (per unit area) at Fifteen Feet, Stony Point Bay, Lake Superior, 1967.

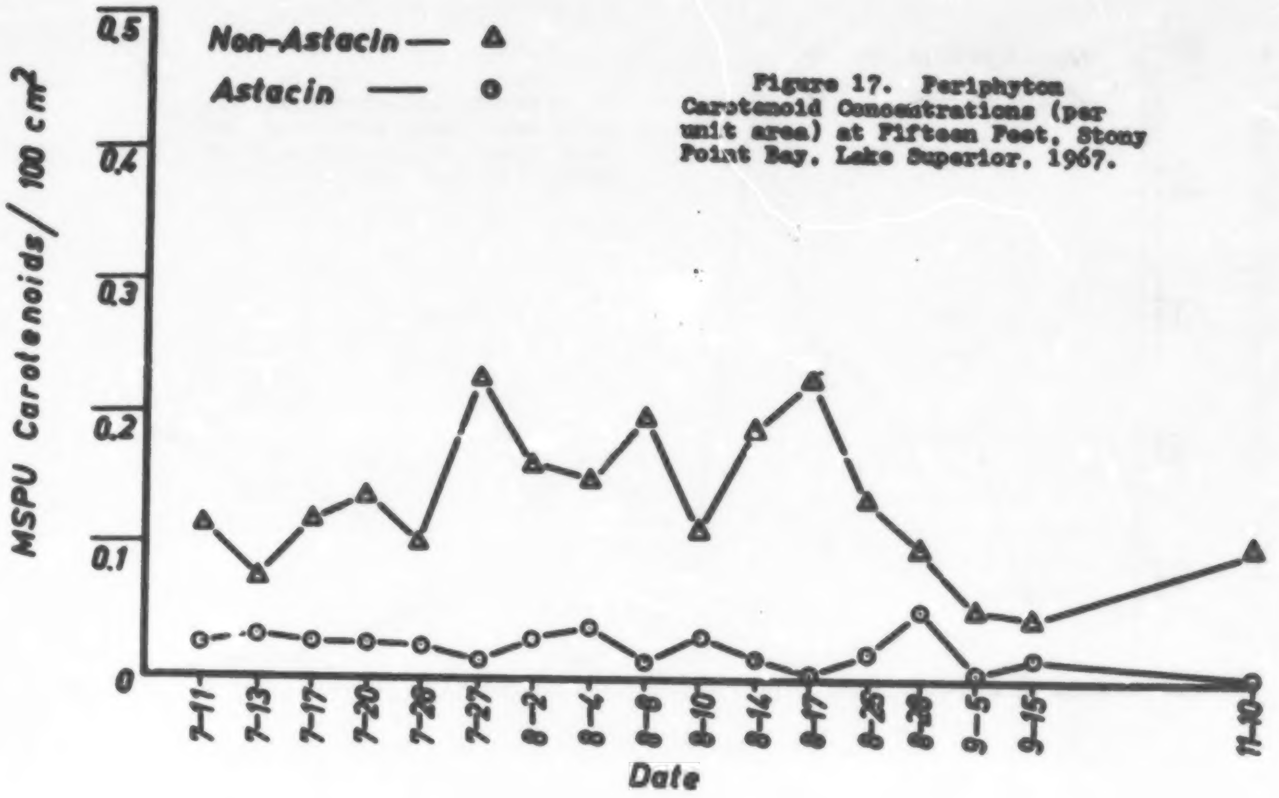

Figure 17. Periphyton Carotenoid Concentrations (per unit area) at Fifteen Feet, Stony Point Bay, Lake Superior, 1967.

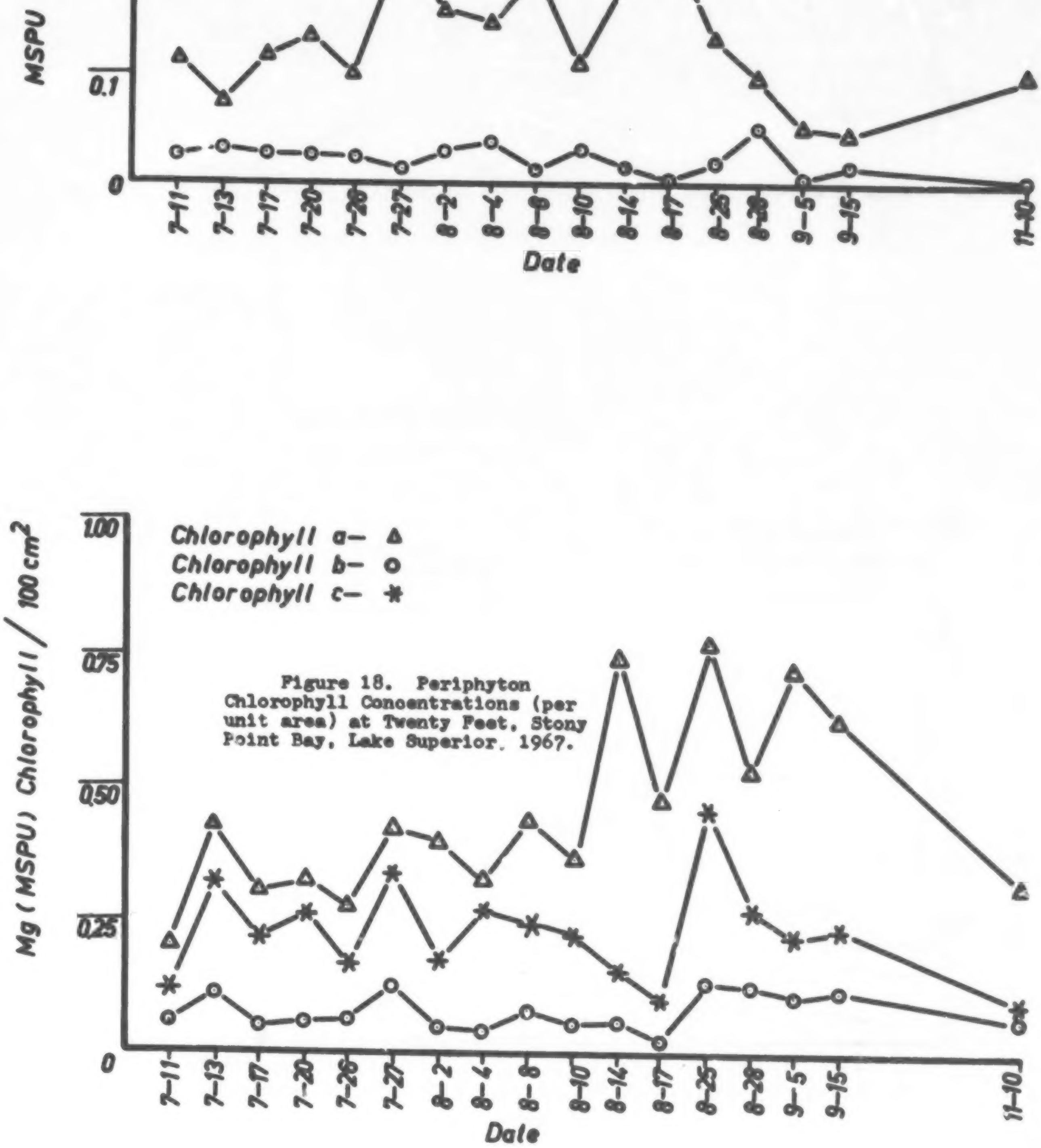

Figure 18. Periphyton Chlorophyll Concentrations (per unit area) at Twenty Feet, Stony Point Bay, Lake Superior, 1967.

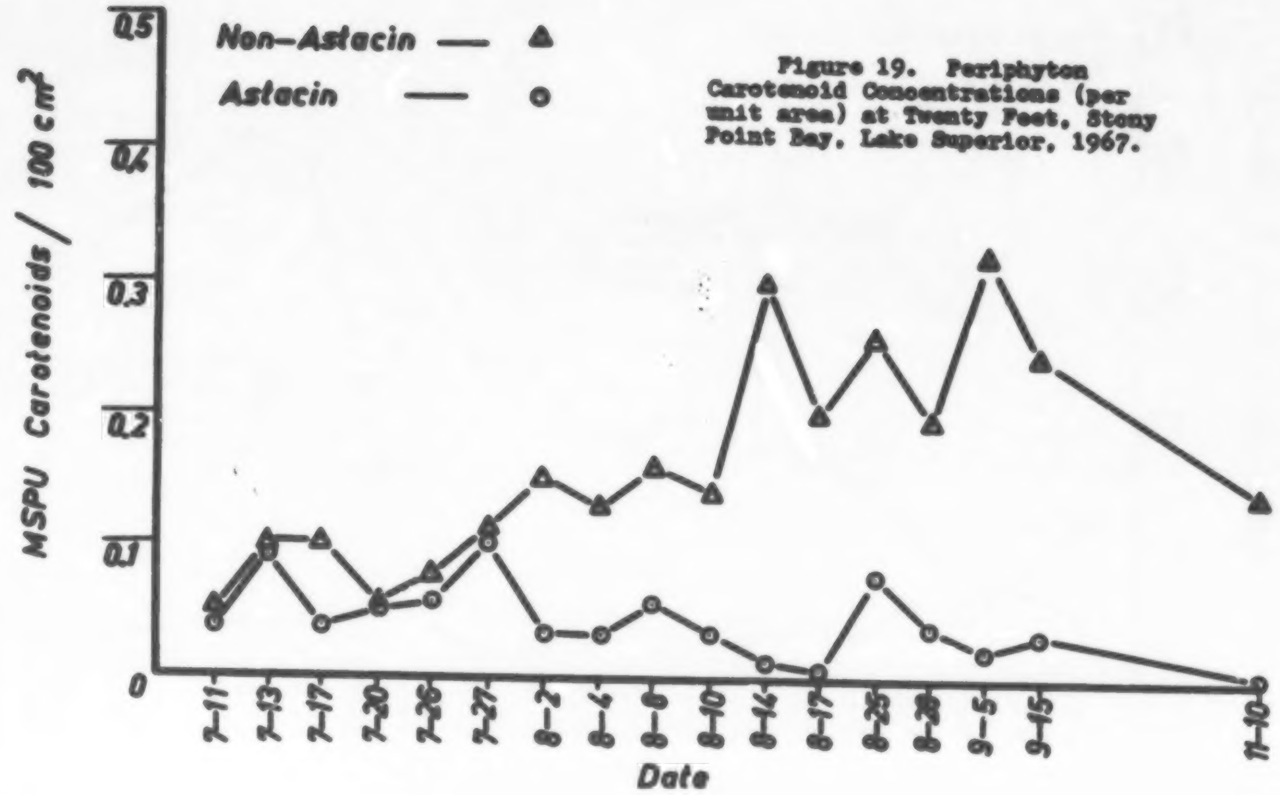

Figure 19. Periphyton Carotenoid Concentrations (per unit area) at Twenty Feet, Stony Point Bay, Lake Superior, 1967.

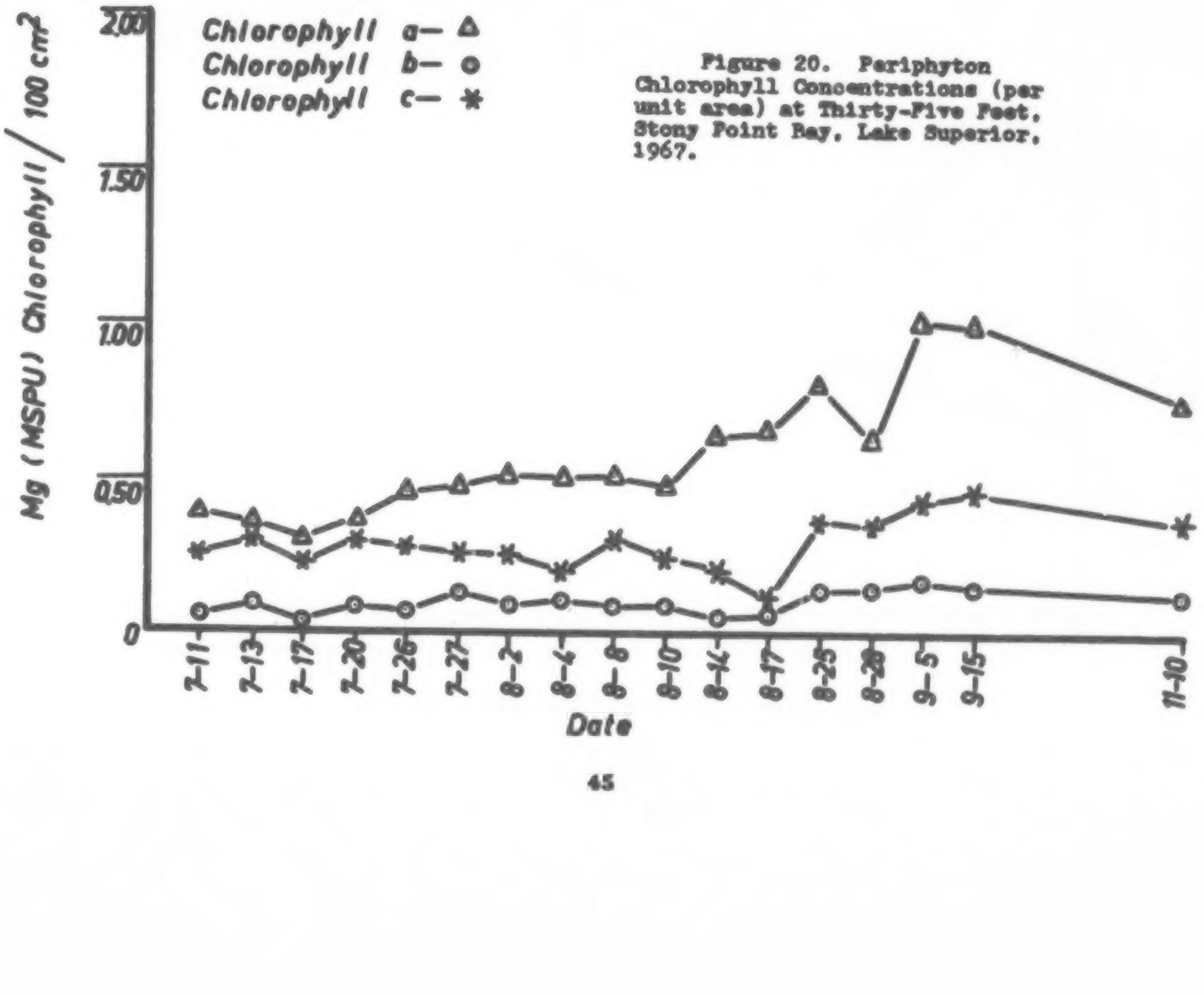

Figure 20. Periphyton Chlorophyll Concentrations (per unit area) at Thirty-Five Feet, Stony Point Bay, Lake Superior, 1967.

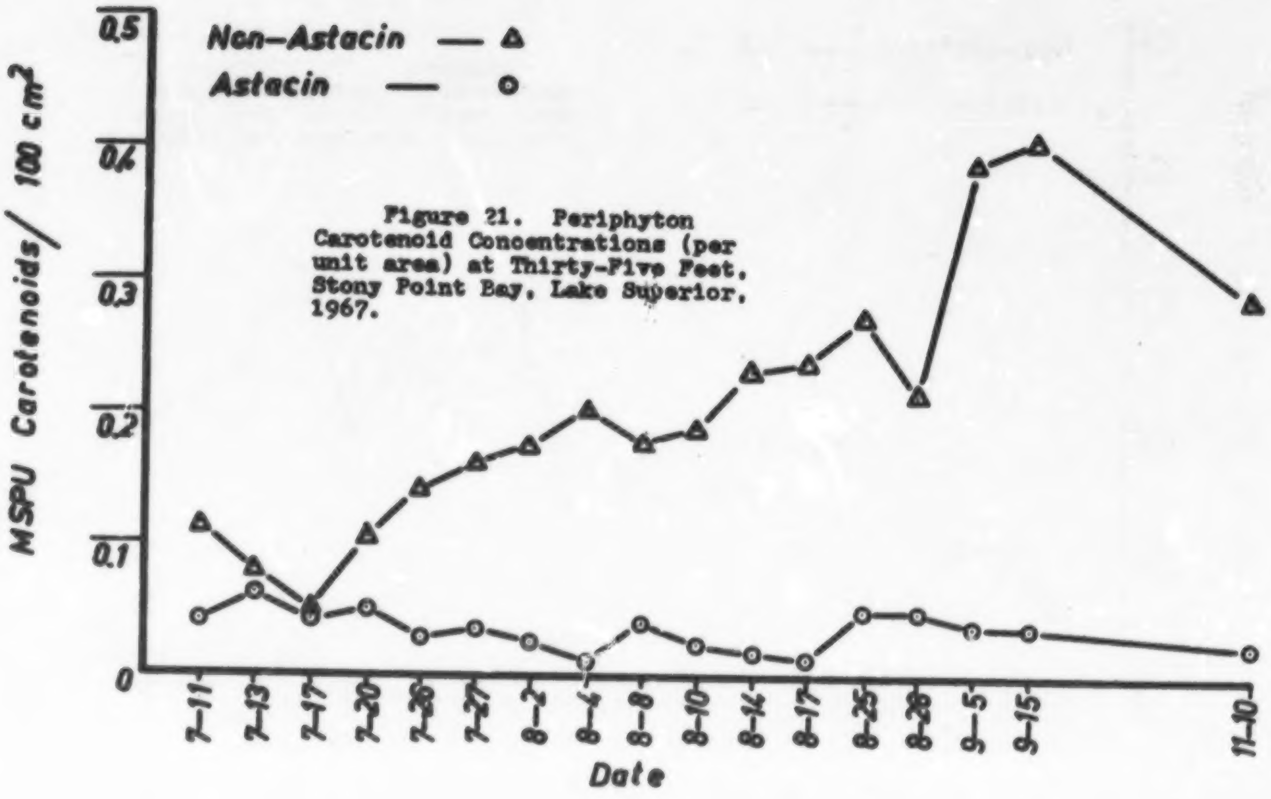

Figure 21. Periphyton Carotenoid Concentrations (per unit area) at Thirty-Five Feet, Stony Point Bay, Lake Superior, 1967.

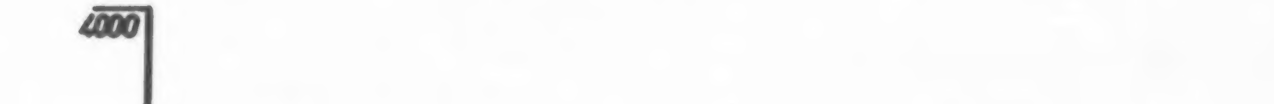

Figure 22. Regression Line, Counts Versus Total Chlorophyll; Naturally Occurring Periphyton at 2.5 Feet, Stony Point Bay, Lake Superior, 1967.

$Y = 1,108,923 + 667,855\ X$

$r = .639$

$P = 0.01$

resent removal of organisms as a result of turbulent water and subsequent regrowth during relatively calm periods. However, the high mean pigment concentrations in the shallow water indicate that the biomass in these areas was never seriously reduced by wave action. Some of the variability in biomass in shallow water may also have been due to a relatively lesser degree of homogeneity in the community in terms of area than in deeper water. The continual rise in pigment concentrations at the twenty and thirty-five foot depths during the summer is probably indicative of a true seasonal increase in biomass, which reached a maximum on September 5. Presumably, the turbulence in shallow water was more severe than that occurring elsewhere, and at the twenty and thirty-five foot depths the turbulence was not of sufficient strength to disturb the periphyton organisms. However, the depression in pigment concentrations on August 28 at all depths indicates that a current affecting all parts of the sampling area developed between August 25 and 28. Such a current might be produced by strong, shifting local winds. Weather data show that rainstorms and winds in excess of twenty-five miles per hour occurred in the sampling area on August 26 and 27. During this period, the winds shifted from south to northwest, and probably produced enough water movement to remove part of the periphyton at all depths in the bay.

Analysis of samples collected on November 10 revealed that the pigment concentrations on a unit area basis had decreased considerably at all depths except ten and fifteen feet, where the concentrations were never particularly high. The highest concentration of pigments was present at a depth of thirty-five feet, while the lowest concentration was encountered at 2.5 feet. For example, chlorophyll *a* ranged from 0.165 milligrams per 100 square centimeters at 2.5 feet to 0.752 milligrams per 100 square centimeters at thirty-five feet. Part of the general decrease in pigment concentrations between September 15 and November 10 may have been due to seasonal reduction in growth; however, since the pigment concentrations were highest at thirty-five feet, it is more likely that a severe storm removed much of the periphyton from the rocks in the shallow water.

The foregoing explanations regarding the variations in pigment concentrations during the summer are valid only if the pigment values are correlated well enough with the numbers of organisms to indicate the general magnitude of biomass at each depth. Correlation coefficients were calculated for total counts and total chlorophyll values for samples from each sampling depth. In addition, to facilitate future estimations of numbers of periphyton organisms based on total chlorophyll concentration, regression lines were constructed using the least squares method. Counts (y axis) were plotted against total chlorophyll values (x axis). The regression lines are presented in Figures 22 through 27, along with the correlation coefficients (r), the probability values (P), and the equations for the slope of each line. The procedures followed in the calculation of correlations and regressions are described in Appendix D. The two parameters were found to be positively correlated at all depths, the correlation coefficients (r) ranging from 0.639 (P=0.01) for samples from the 2.5 foot depth to 0.921 (P=0.001) for samples from a depth of thirty-

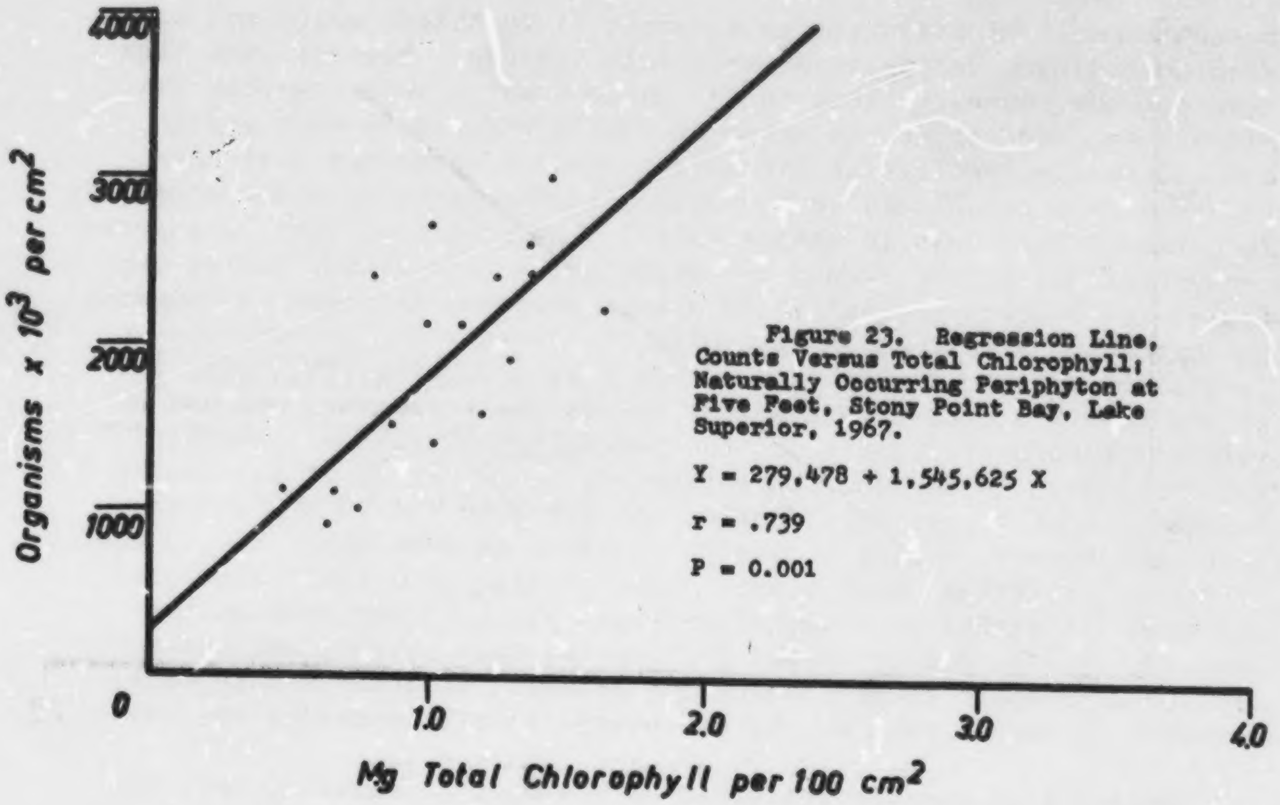

Figure 23. Regression Line, Counts Versus Total Chlorophyll; Naturally Occurring Periphyton at Five Feet, Stony Point Bay, Lake Superior, 1967.

Y = 279,478 + 1,545,625 X

r = .739

P = 0.001

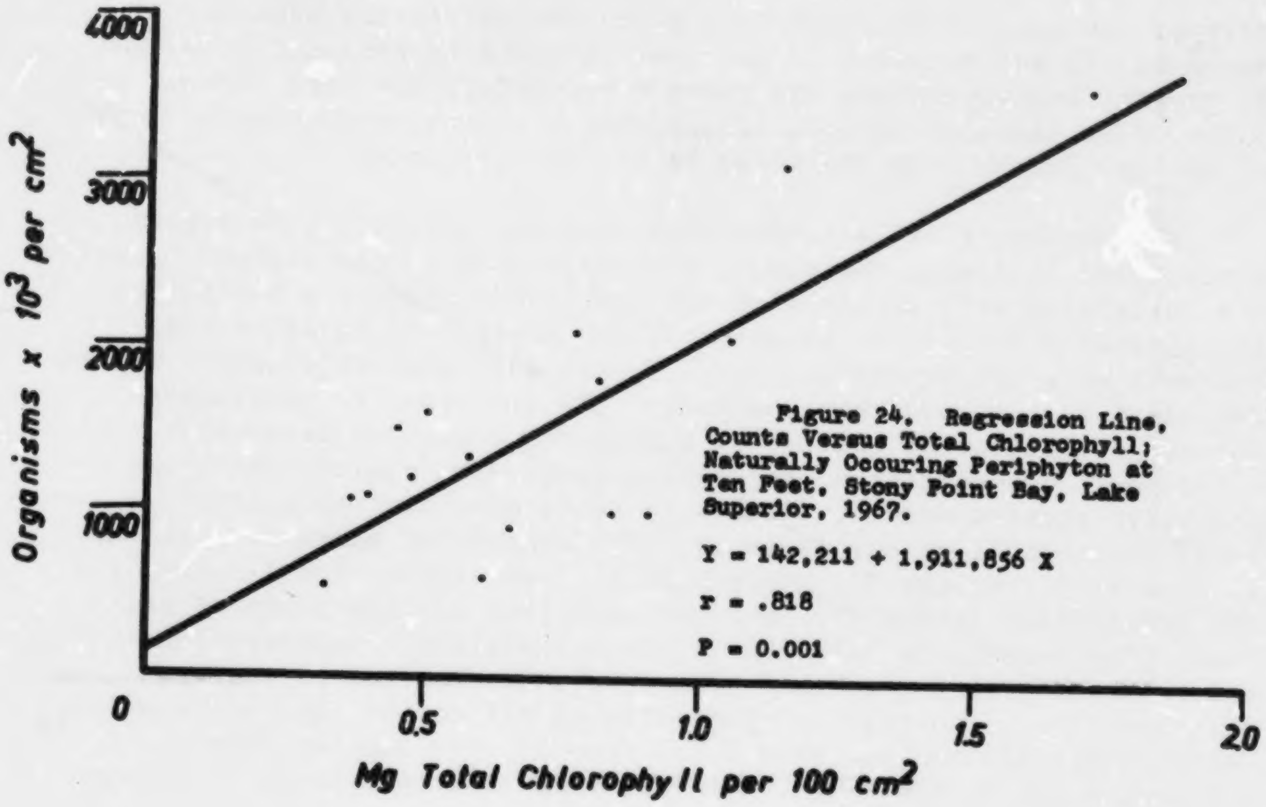

Figure 24. Regression Line, Counts Versus Total Chlorophyll; Naturally Occuring Periphyton at Ten Feet, Stony Point Bay, Lake Superior, 1967.

Y = 142,211 + 1,911,856 X

r = .818

P = 0.001

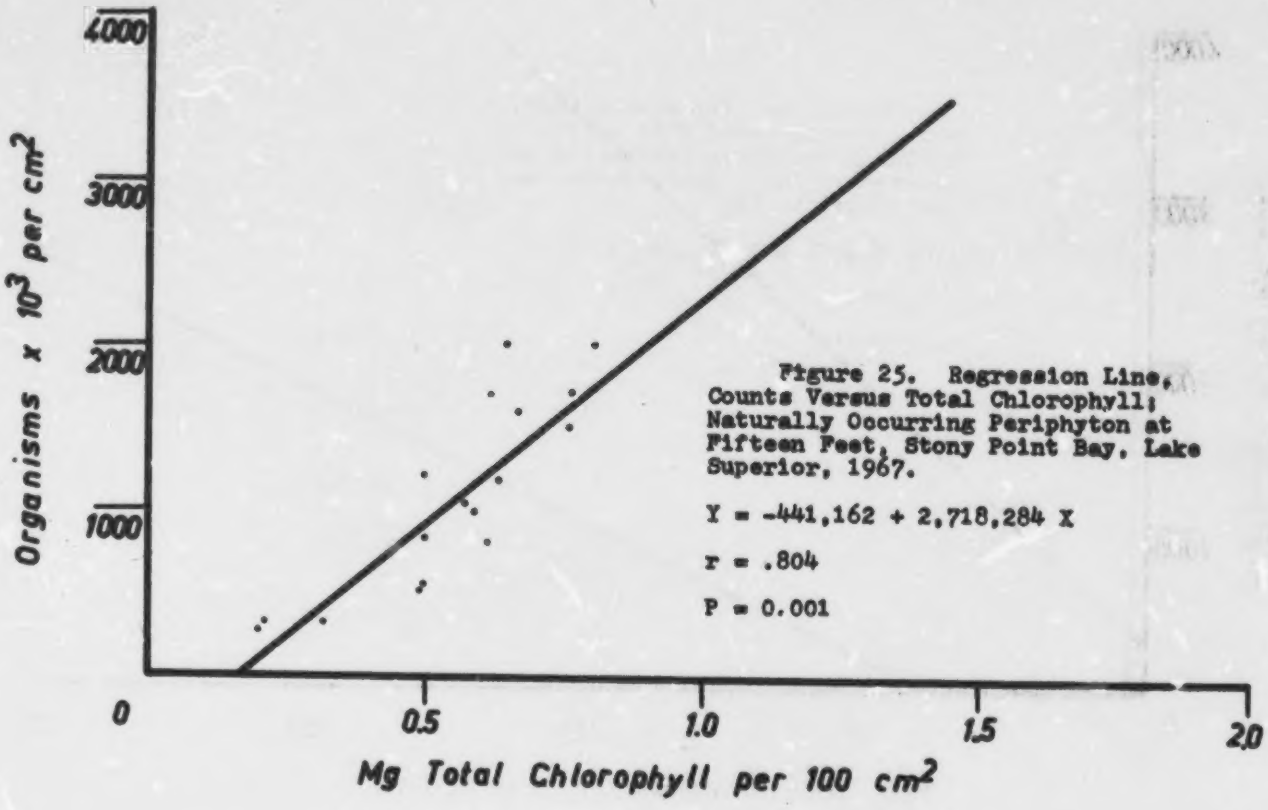

Figure 25. Regression Line, Counts Versus Total Chlorophyll; Naturally Occurring Periphyton at Fifteen Feet, Stony Point Bay, Lake Superior, 1967.

Y = -441,162 + 2,718,284 X

r = .804

P = 0.001

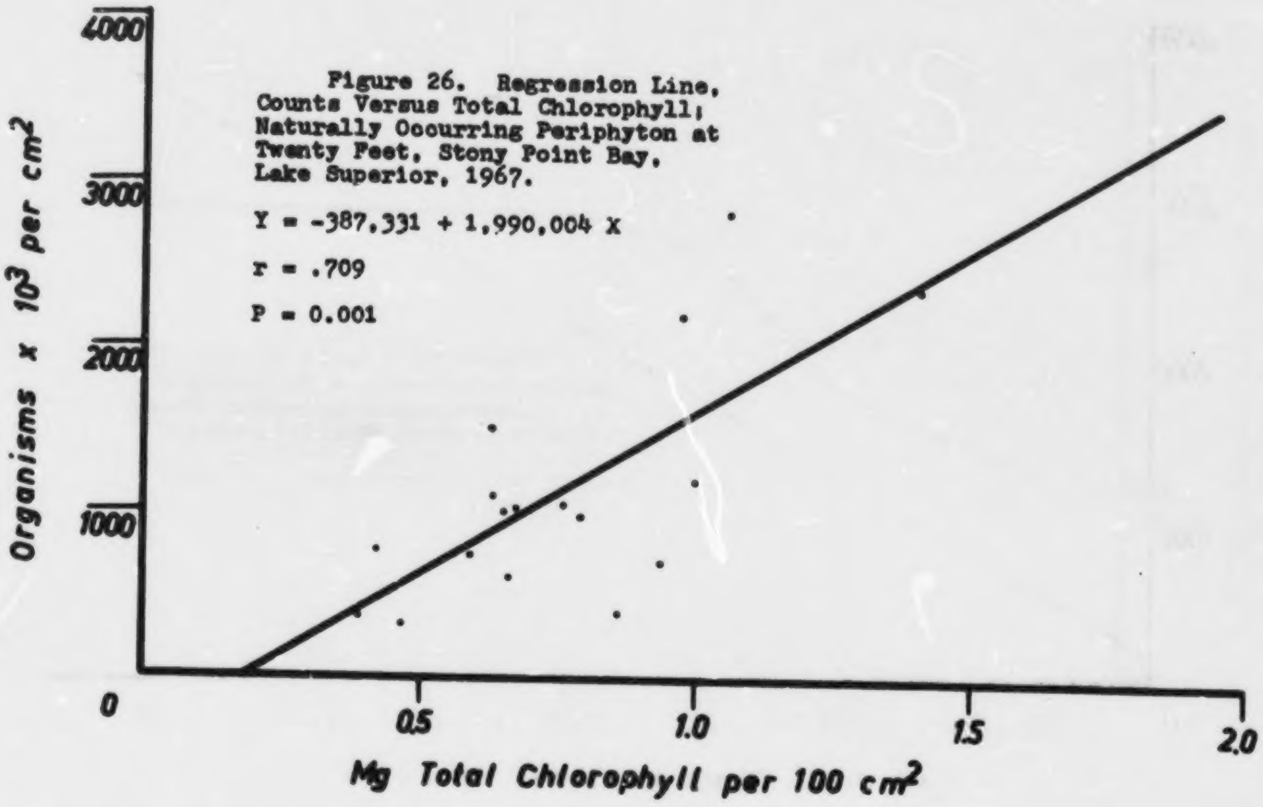

Figure 26. Regression Line, Counts Versus Total Chlorophyll; Naturally Occurring Periphyton at Twenty Feet, Stony Point Bay, Lake Superior, 1967.

Y = -387,331 + 1,990,004 X

r = .709

P = 0.001

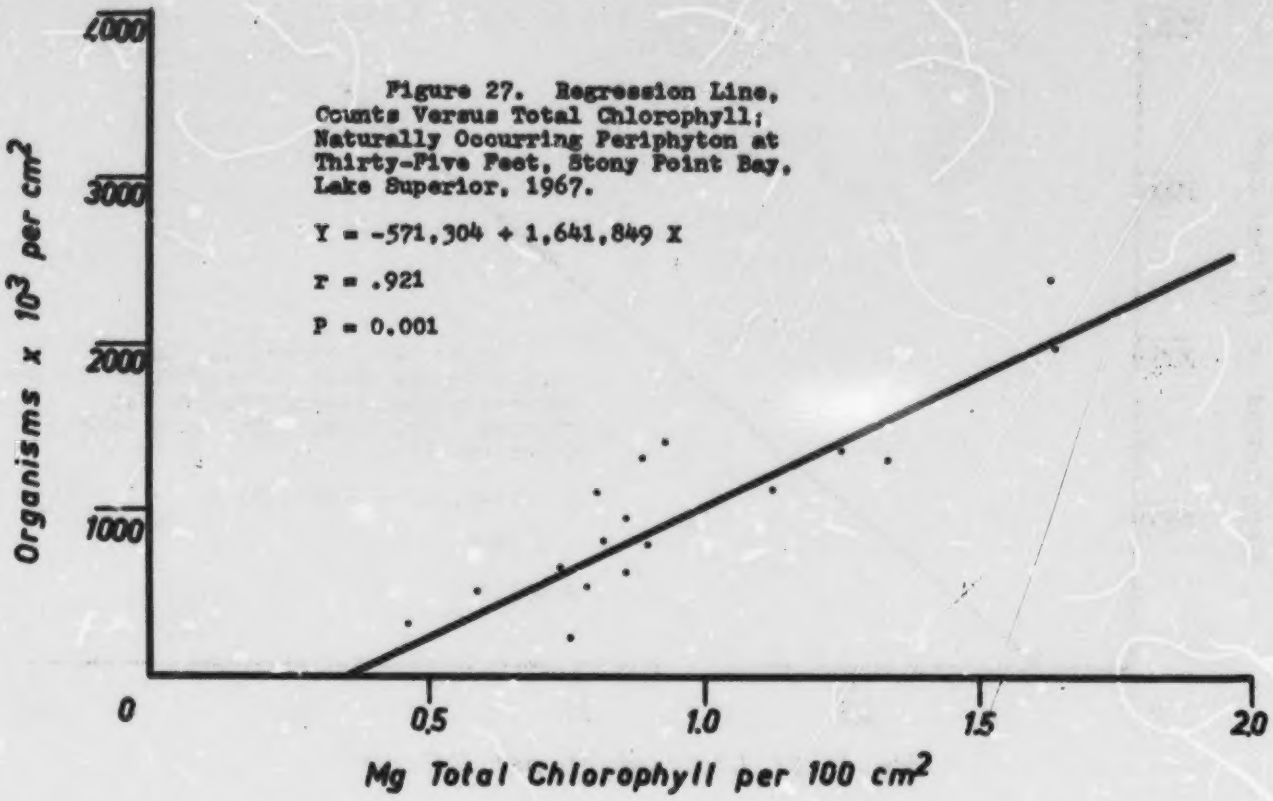

Figure 27. Regression Line, Counts Versus Total Chlorophyll; Naturally Occurring Periphyton at Thirty-Five Feet, Stony Point Bay, Lake Superior, 1967.

$Y = -571,304 + 1,641,849\ X$

$r = .921$

$P = 0.001$

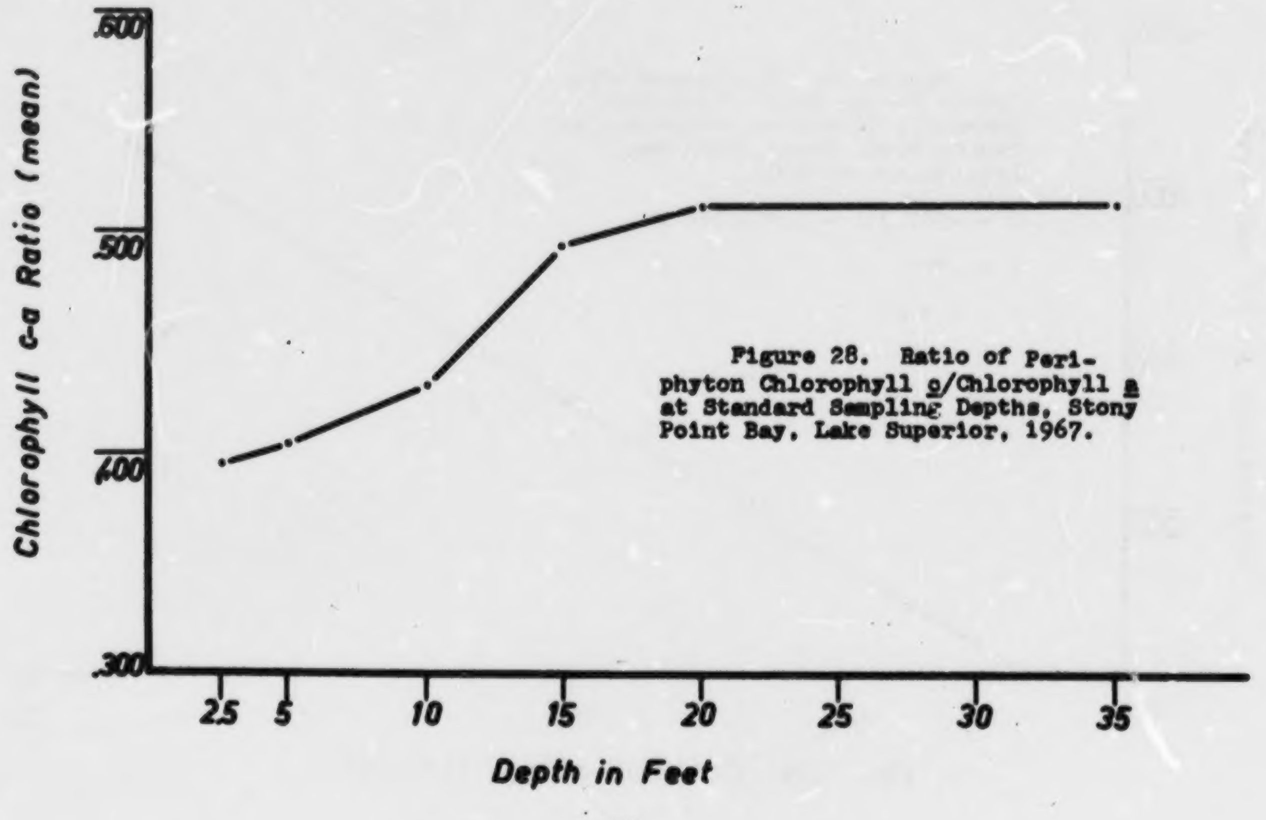

Figure 28. Ratio of Periphyton Chlorophyll c/Chlorophyll a at Standard Sampling Depths, Stony Point Bay, Lake Superior, 1967.

five feet. The correlation was generally better for samples from the deeper water. It should be understood that these rather close correlations do not contradict the findings which show differences in amount of pigment per unit of ash-free dry weight from one depth to another. The correlations and regressions were determined for each depth and do not reflect any differences related to depth. A regression line based on all counts and pigment concentrations irrespective of depth would be useless in light of the fact that different relationships exist between the two values at each depth. However, numbers of organisms in Stony Point Bay may be predicted from total chlorophyll data when the sampling depth is known and the proper regression line is used. The results of such predictions may be expected to be more accurate for samples from deep water than for those from shallow water.

The mean ratio of chlorophyll c/chlorophyll a was 0.459 for the entire bay in 1967. However, the values calculated for each depth range from 0.395 at 2.5 feet to 0.511 at thirty-five feet (see Figure 28). In contrast, the ratio of non-astacin carotenoids/chlorophyll a decreased with increasing depth, varying from 0.486 at 2.5 feet to 0.344 at thirty-five feet (Figure 29); the mean for the entire bay was 0.415. The same phenomenon, i.e., a decrease in the ratio of carotenoids/chlorophyll a as depth increases, has been reported for stratified marine phytoplankton by Ryther et al. (1958). If the species composition of the periphyton were very similar at all depths in the bay, it could be assumed that observed differences in pigment ratios in large samples of the community were a result of differences in the pigment ratios in individual organisms of the same type. It could be further assumed that these differences were due to environmental factors. The species composition of the periphyton community at all depths in Stony Point Bay was very constant (Fox, 1969), with diatoms making up over ninety per cent of the population. Percentages of the various types of organisms varied little with depth, so the composition of the community at different depths is not important in explaining varying pigment ratios. With this fact established, other possible reasons for differences in pigment ratios at various depths can be explored. Table VI shows that both chlorophyll a and chlorophyll c increased in relation to ash-free dry weight as depth became greater; however, the amount of chlorophyll a per unit of organic weight is increased by only thirty-four per cent from 2.5 feet to thirty-five feet, while chlorophyll c is increased by seventy-four per cent. This difference accounts for the rising chlorophyll c/a ratio as depth is increased. There is virtually no difference in the concentration of non-astacin carotenoids in relation to ash-free dry weight at the standard sampling depths (a decrease of five per cent from 2.5 feet to thirty-five feet). The decreasing ratio of carotenoids/chlorophyll a as depth increased is a result only of the rising chlorophyll a concentration.

The rise in pigment concentrations in relation to organic weight as depth is increased may be viewed as a response to lower light intensity. The average mid-day light intensity at each sampling depth for 1967 is shown graphically in Figure 30. Each point represents

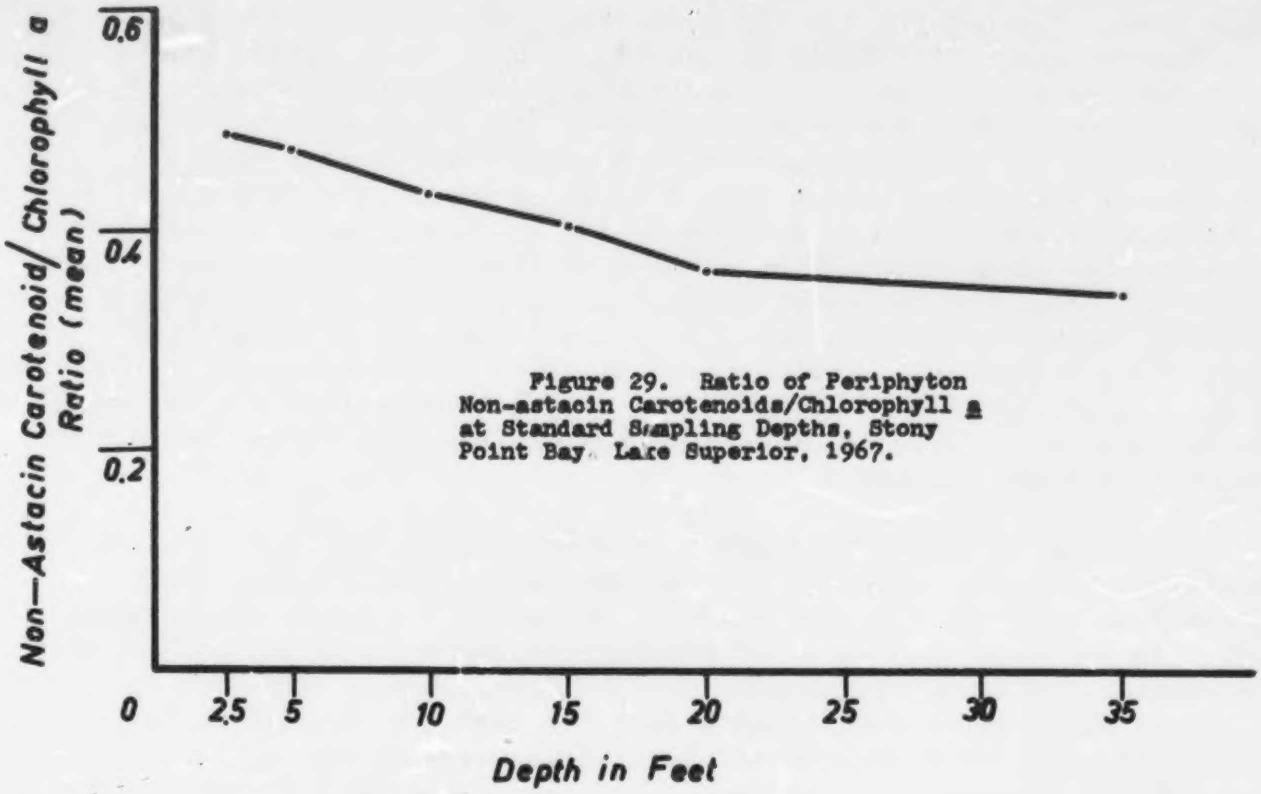

Figure 29. Ratio of Periphyton Non-astacin Carotenoids/Chlorophyll a at Standard Sampling Depths, Stony Point Bay, Lake Superior, 1967.

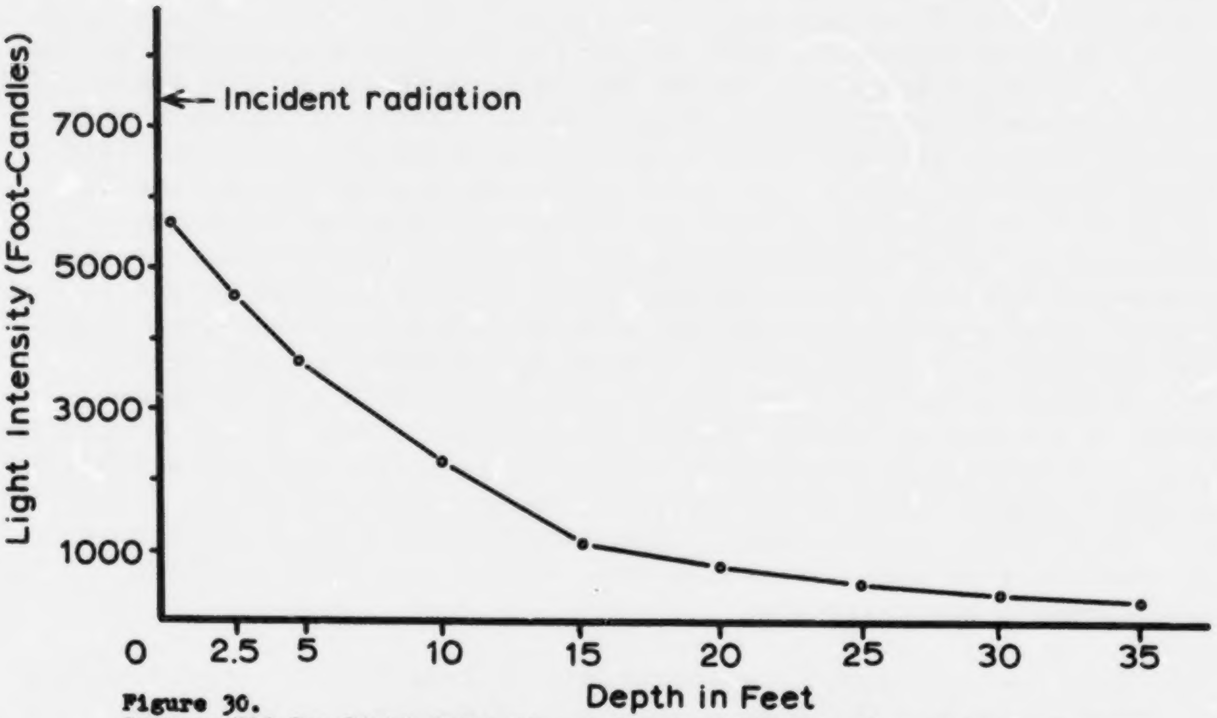

Figure 30.
Average Mid-Day Light Intensity at Standard Depths, Stony Point Bay, Lake Superior; June - September, 1967.

TABLE VI

PERIPHYTON PIGMENT CONCENTRATIONS IN RELATION TO ASH-FREE DRY WEIGHT AT STANDARD DEPTHS, STONY POINT BAY, LAKE SUPERIOR, 1967

Depth	Mg pigment x 10^{-3}/mg ash-free dry weight		
	Chlorophyll *a*	Chlorophyll *c*	Non-astacin carotenoids
2.5 feet	3.62	1.42	1.76
5	3.50	1.43	1.64
10	3.79	1.64	1.65
15	3.64	1.79	1.45
20	4.65	1.94	1.64
35	4.86	2.48	1.67

TABLE VII

SEASONAL VARIATION OF PERIPHYTON PIGMENT RATIOS STONY POINT BAY, LAKE SUPERIOR, 1967 (ALL DEPTHS COMBINED)

Date	$\frac{\text{Chlorophyll c}}{\text{Chlorophyll a}}$	$\frac{\text{Chlorophyll b}}{\text{Chlorophyll a}}$	$\frac{\text{Non-astacin carotenoids}}{\text{Chlorophyll a}}$
7-11	.588	.115	.348
7-13	.611	.208	.364
7-17	.636	.163	.372
7-20	.677	.222	.408
7-26	.591	.195	.324
7-27	.511	.214	.428
8-2	.522	.171	.391
8-4	.510	.190	.417
8-8	.384	.129	.428
8-10	.460	.181	.431
8-14	.227	.072	.424
8-17	.242	.059	.453
8-25	.464	.160	.383
8-28	.622	.263	.383
9-5	.284	.224	.452
9-15	.342	.164	.418

an average of the readings taken on each of the seventeen sampling days. The average intensity at the surface of the water was 7275 foot-candles. Six inches of water lowered the reading to 5600 foot-candles. From this point the average readings decreased gradually with depth, reaching a minimum of 265 foot-candles at a depth of thirty-five feet. The readings at each depth were quite variable, depending on atmospheric conditions and the effects of turbidity on the day a measurement was made. It has been shown that visible light of relatively short wavelength penetrates deeper into pure water than light of longer wavelength; the same phenomenon, with certain variations, occurs in water containing dissolved and suspended solids (Clarke, 1954). Since the major absorption peak in the red band for chlorophyll c is at a lower wavelength than the peak for chlorophyll a, the preferential increase in chlorophyll c by the periphyton as light intensity decreases may be a response to the greater proportion of shorter wavelength light in deep water.

In order to determine whether or not the various pigment ratios changed during the season, the ratios were calculated on the basis of combined pigment concentrations from all depths for each sampling day. The ratios of chlorophyll c, chlorophyll b, and non-astacin carotenoids, respectively, to chlorophyll a for each day are presented in Table VII. The chlorophyll c/a ratios exhibit considerable variation, but no seasonal trend is apparent. The ratio of non-astacin carotenoids to chlorophyll a is quite constant; a slight upward trend during the summer is indicated. It is reasonable that the chlorophyll c/a ratio was much more erratic on a seasonal basis than the carotenoid/chlorophyll a ratio, since the concentration of chlorophyll c seems to be subject to control by the intensity or spectral composition of light. The changes in the c/a ratio during the sampling period may be indicative of variable light intensity due to turbidity. The ratios of chlorophyll b to chlorophyll a, which should reflect the relative numbers of green algae present in the samples, are quite variable and show no particular trend. The highest ratio occurred on August 28 and the lowest on August 17.

The dry weights and ash-free dry weights of all periphyton samples collected from Stony Point Bay in 1967 are presented in Tables VIII and IX. The seasonal variation of the ash-free dry weights at each sampling depth is shown graphically in Figures 31 through 36. Each weight may be compared directly to a corresponding pigment concentration, since samples for both determinations were taken from the same periphyton suspension. The mean dry weight per unit area of rock surface was highest for samples from a depth of 2.5 feet and lowest for those from thirty-five feet (Table VIII). The dry weights decreased with increasing depth, except between fifteen and twenty feet, where the average weights were nearly identical. The highest mean ash-free dry weight, 2.7 milligrams per square centimeter, occurred at 2.5 feet, while the lowest, 0.91 milligrams per square centimeter, was recorded at fifteen feet (Table IX). The weights increased slightly from fifteen to thirty-five feet. The ash-free dry weights of the 1967 samples were found to be well correlated with total counts of organisms. However, as shown by

TABLE VIII

NATURALLY OCCURRING PERIPHYTON DRY WEIGHTS AT THE STANDARD SAMPLING DEPTHS
STONY POINT BAY, LAKE SUPERIOR, 1967
MILLIGRAMS PER SQUARE CENTIMETER OF ROCK SURFACE

Date	Sampling depth in feet					
	2.5	5	10	15	20	35
7-11	28.8	7.4	9.0	7.8	3.3	6.0
7-13	30.0	8.7	4.4	6.2	9.2	7.9
7-17	19.7	26.1	9.6	6.1	7.4	-*
7-20	33.3	10.7	10.5	10.8	4.7	8.1
7-26	39.8	18.4	16.5	14.5	8.1	8.4
7-27	38.9	17.2	17.7	15.2	7.2	7.3
8-2	28.9	14.4	16.2	17.6	8.5	11.0
8-4	14.8	5.9	12.7	18.8	13.8	9.0
8-8	21.2	19.8	10.4	11.3	27.8	10.5
8-10	12.5	20.3	9.0	10.6	11.5	10.4
8-14	27.9	11.7	9.2	16.7	15.8	10.9
8-17	21.4	13.6	14.3	17.9	12.1	10.5
8-25	21.9	36.0	44.3	14.0	20.3	13.9
8-28	23.3	29.6	10.5	14.8	9.3	13.6
9-5	52.0	21.5	12.1	4.8	13.7	19.6
9-15	39.5	28.8	10.7	3.1	17.5	17.2
11-10	21.3	21.3	17.5	13.4	17.0	13.8
Mean	27.9	18.2	13.8	11.9	12.1	10.4

*Sample was lost

TABLE IX

NATURALLY OCCURRING PERIPHYTON ASH-FREE DRY WEIGHTS AT THE STANDARD SAMPLING DEPTHS
STONY POINT BAY, LAKE SUPERIOR, 1967
MILLIGRAMS PER SQUARE CENTIMETER OF ROCK SURFACE

Date	Sampling depth in feet					
	2.5	5	10	15	20	35
7-11	3.63	1.37	1.23	1.02	0.64	1.14
7-13	2.53	1.62	0.58	0.63	0.63	0.63
7-17	1.90	1.75	0.98	0.46	0.84	-*
7-20	2.90	1.80	1.03	0.85	0.47	0.69
7-26	3.39	2.04	2.00	1.22	1.05	1.05
7-27	3.95	3.04	1.38	1.11	0.30	0.96
8-2	2.46	1.96	2.07	1.29	0.97	1.04
8-4	2.88	1.10	1.12	1.22	0.97	1.09
8-8	2.09	1.70	1.19	1.10	1.97	1.58
8-10	2.43	2.28	0.71	0.55	0.72	0.80
8-14	2.77	1.46	0.52	0.93	1.08	0.82
8-17	2.66	1.28	1.01	0.77	0.72	1.61
8-25	2.58	2.32	2.25	1.01	1.66	1.18
8-28	2.72	2.27	1.38	1.81	1.04	1.48
9-5	3.86	1.72	1.50	0.88	1.82	2.32
9-15	2.96	2.78	0.81	0.33	1.25	1.65
11-10	0.33	1.13	0.85	0.44	0.55	1.17
Mean	2.70	1.92	1.21	0.91	0.98	1.20

*Sample was lost

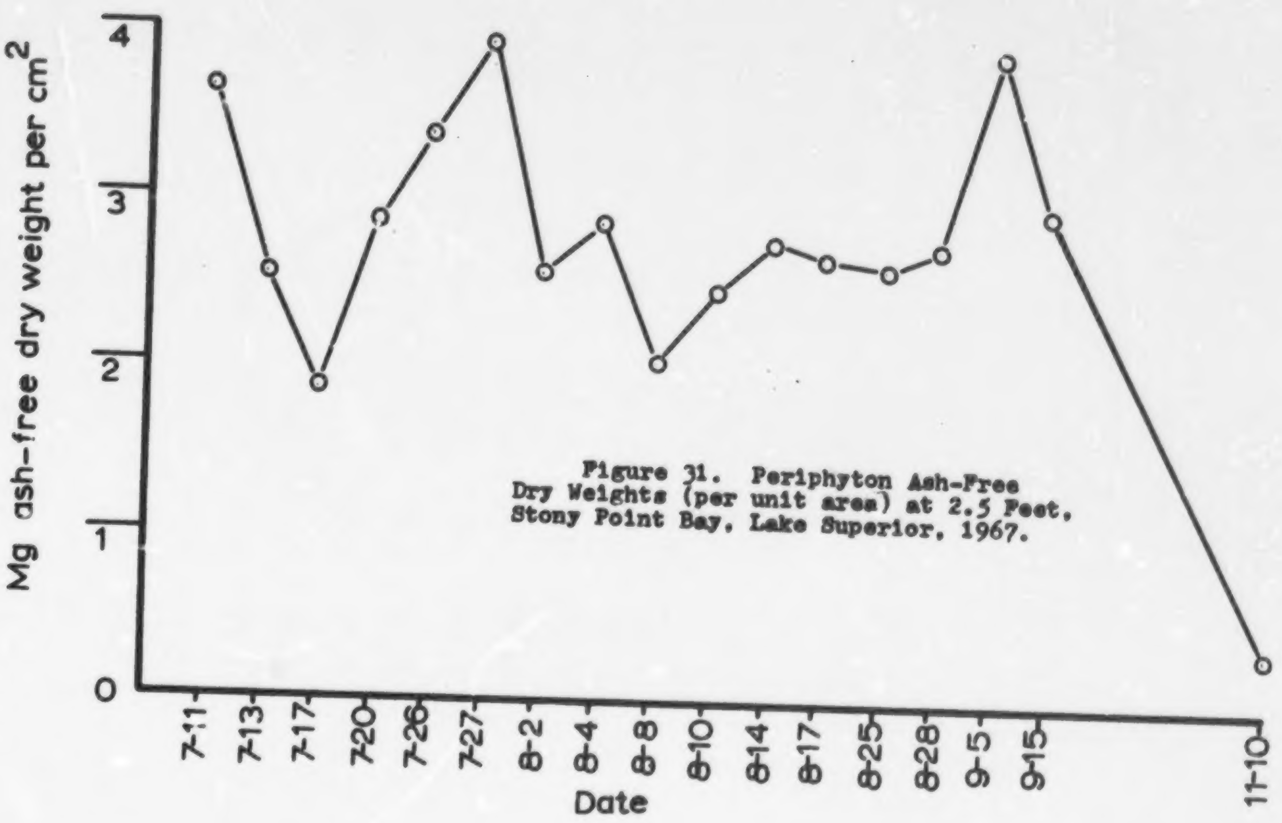

Figure 31. Periphyton Ash-Free Dry Weights (per unit area) at 2.5 Feet, Stony Point Bay, Lake Superior, 1967.

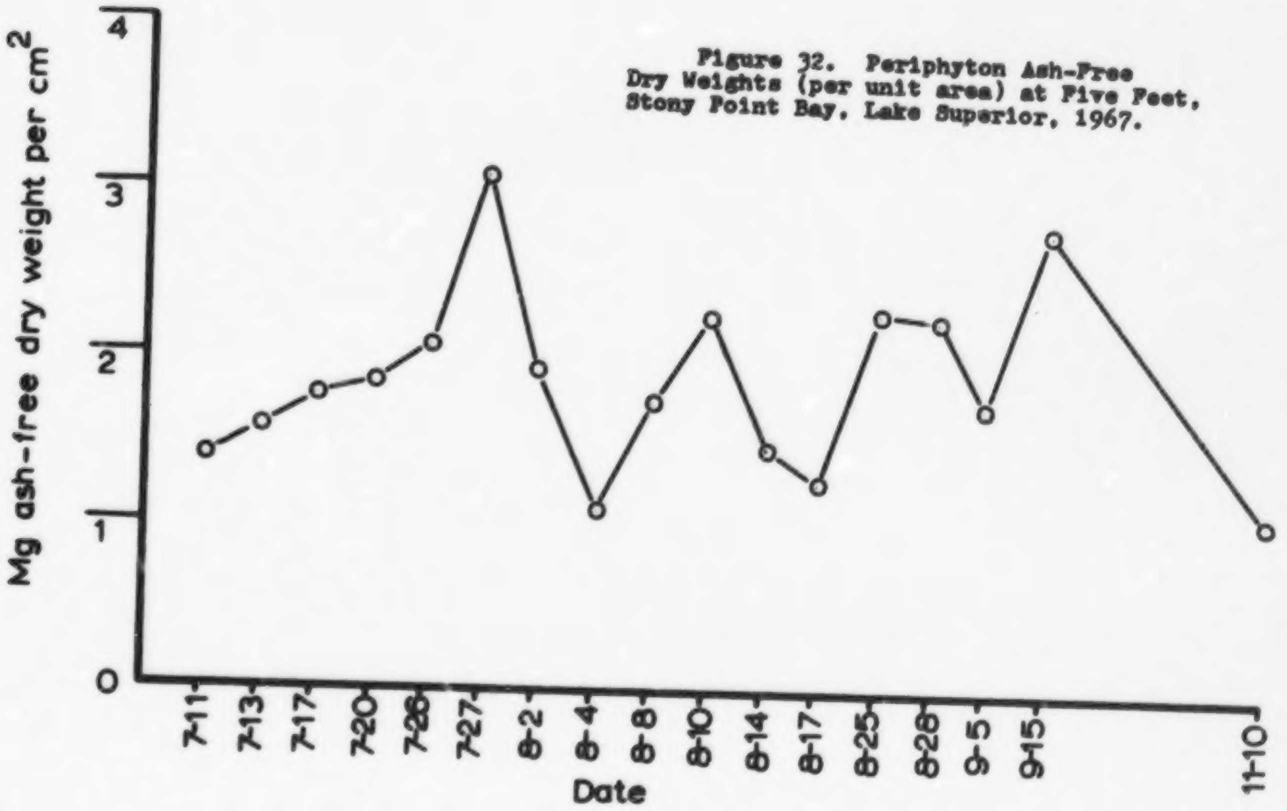

Figure 32. Periphyton Ash-Free Dry Weights (per unit area) at Five Feet, Stony Point Bay, Lake Superior, 1967.

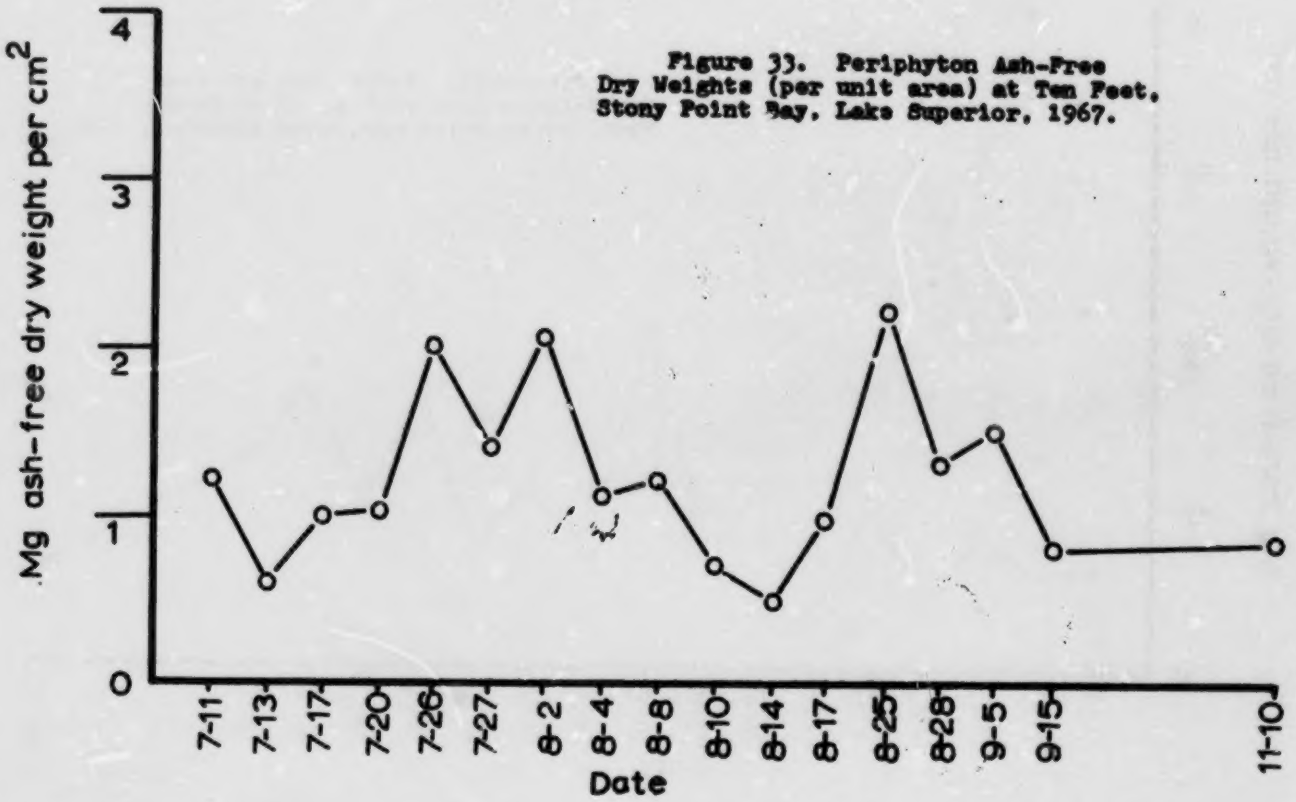

Figure 33. Periphyton Ash-Free Dry Weights (per unit area) at Ten Feet, Stony Point Bay, Lake Superior, 1967.

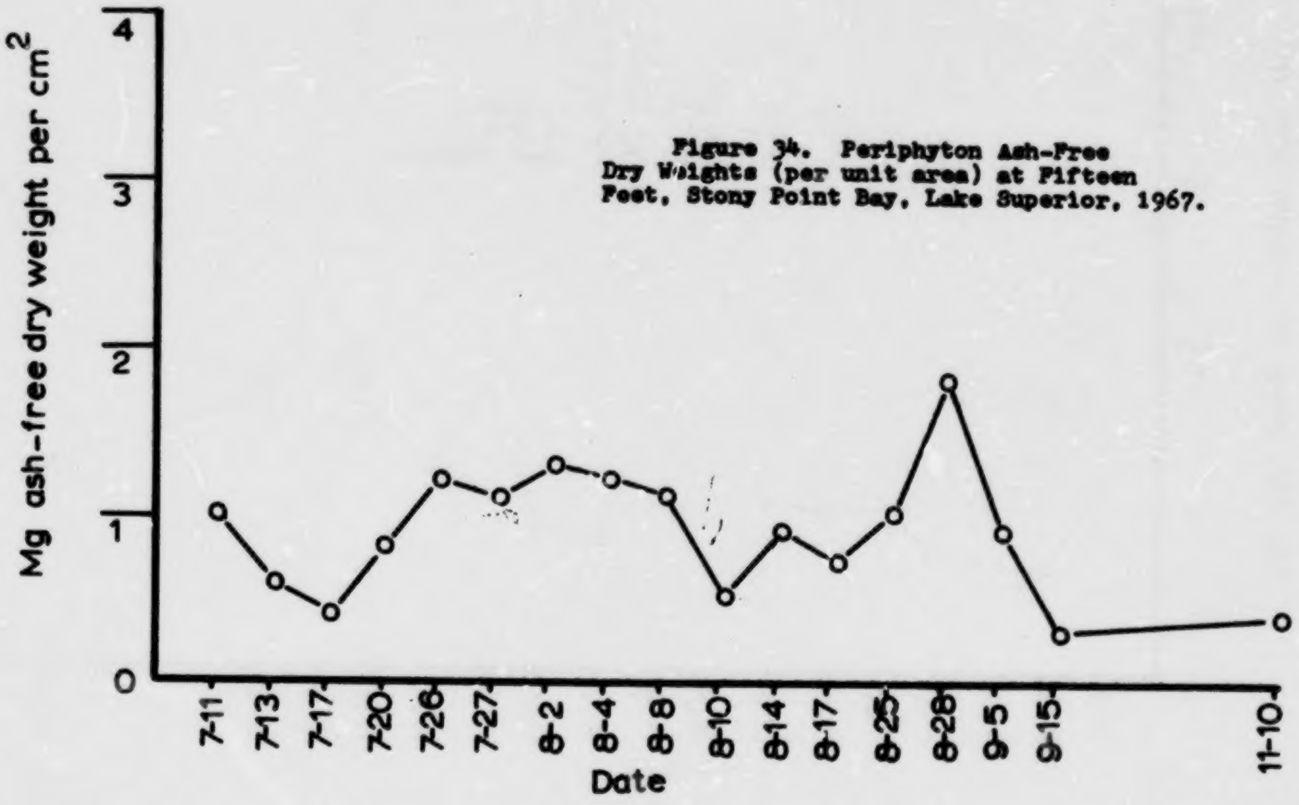

Figure 34. Periphyton Ash-Free Dry Weights (per unit area) at Fifteen Feet, Stony Point Bay, Lake Superior, 1967.

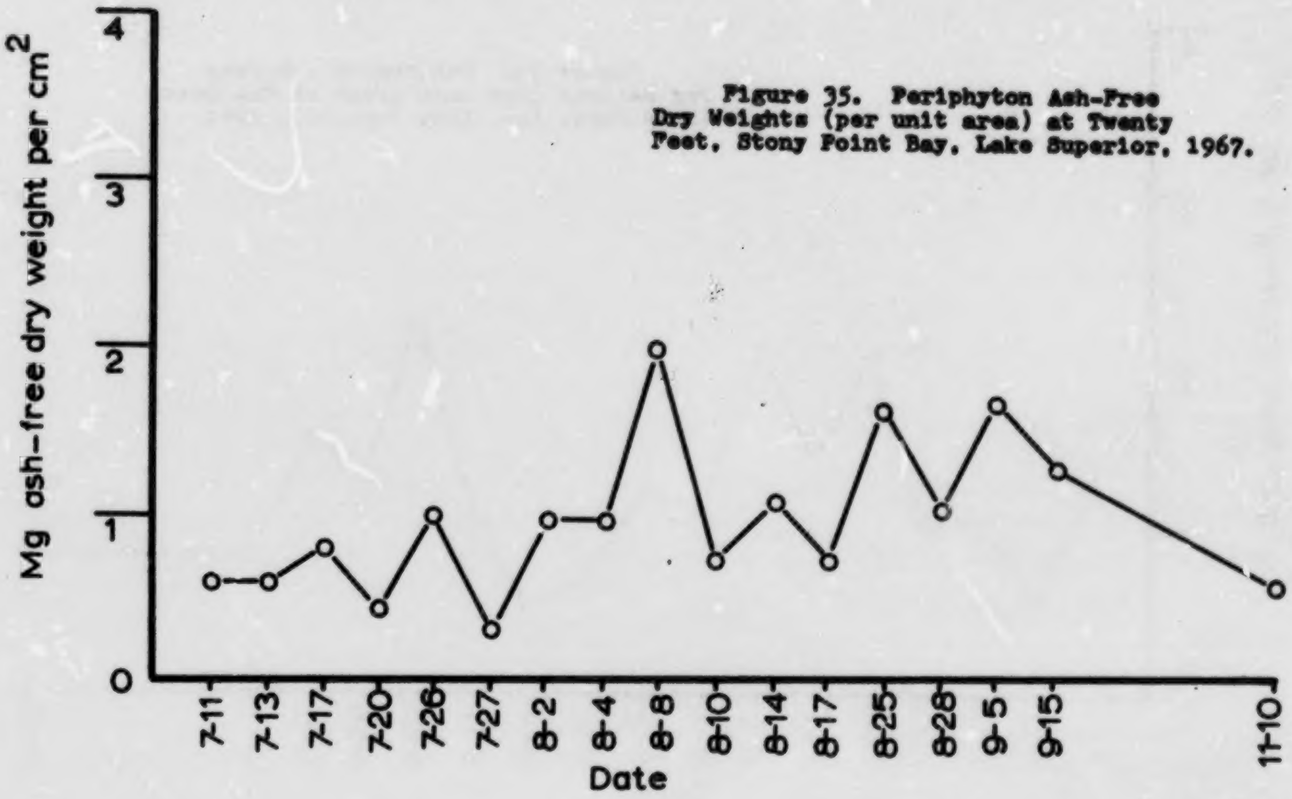

Figure 35. Periphyton Ash-Free Dry Weights (per unit area) at Twenty Feet, Stony Point Bay, Lake Superior, 1967.

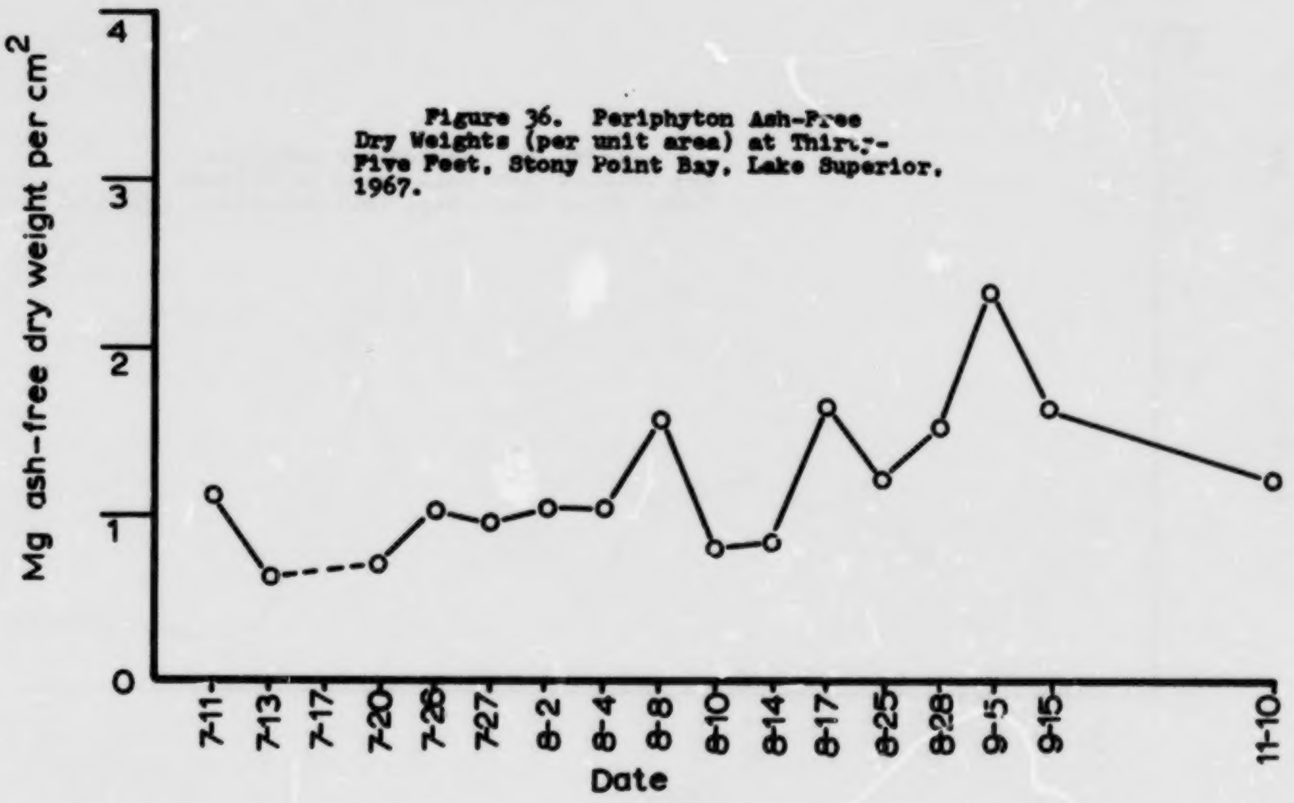

Figure 36. Periphyton Ash-Free Dry Weights (per unit area) at Thirty-Five Feet, Stony Point Bay, Lake Superior, 1967.

Figure 9, the relationship between the organic weights and pigment concentrations was not constant at all depths.

On the basis of the average dry weight of all samples taken during 1967, the total dry weight of the periphyton in Stony Point Bay was calculated to be 55.5 tons (156 grams per square meter). The corresponding ash-free dry weight was 4.4 tons (12 grams per square meter), or 7.9 per cent of the total dry weight. The mild weather of 1967 was probably the main reason why the total dry weight (55.5 tons) was higher than that produced in 1966 (37.1 tons). Since the 1966 samples seemed to contain more sand and clay than the 1967 samples, the actual difference in weight may have been somewhat greater.

It has been suggested that low temperature may be part of the reason for less extensive growths of periphyton in the deeper water of Stony Point Bay. Temperature data for 1967 show that the deeper water was in fact colder than the shallow water (see Table X). Water temperatures were taken each sampling day at every sampling depth as well as at a point just below the surface of the water. It is obvious that the water temperatures decreased with increasing depth throughout the summer. The values at 2.5 feet ranged from 6.5° C. to 19.5° C. The minimum and maximum temperatures were slightly lower at each depth from five feet to twenty feet. The biggest difference was usually between twenty and thirty-five feet. The temperatures at all depths increased continually during the first two-thirds of the sampling period, reaching a maximum on August 14. After that date, the temperatures tended to decrease slightly at all depths except twenty and thirty-five feet. At the twenty foot depth, the maximum temperature, 14.0° C., was recorded on August 14, and again on September 15. The thirty-five foot maximum, 9.5° C., occurred on August 14, 25, 28, and September 5. Even at these times, the temperatures at 2.5, 5, and 10 feet were about twice as high as the thirty-five foot value. On November 10, the temperatures at all depths in the bay were very similar to those recorded on the first day of the sampling period, July 11.

The average gross photosynthetic rate of periphyton organisms taken from each depth in Stony Point Bay is presented in Figure 37. The values are reported in terms of microliters of oxygen evolved per hour per square centimeter of rock surface and were determined manometrically at 20° C. and at a light intensity of 1500 foot-candles. Samples from 2.5 feet produced the highest mean rate of oxygen evolution (44.6 microliters per hour per square centimeter). Samples from each successive depth evolved less oxygen per hour than the preceding ones, except the twenty foot samples, which produced slightly more than the fifteen foot samples. The mean production rate for the samples from thirty-five feet was only 15.3 microliters of oxygen per hour per square centimeter. The 1967 values were lower than those recorded for Stony Point Bay in 1966. This difference probably occurred because no carbon dioxide was added to the atmosphere above the reaction flasks in the respirometer. None was added because it seemed to slow the equilibration of gas phases in the system

TABLE X

TEMPERATURES AT THE STANDARD DEPTHS
STONY POINT BAY, LAKE SUPERIOR, 1967
DEGREES CENTIGRADE

Date	Depth in Feet						
	Surface	2.5	5	10	15	20	35
7-11	6.5	6.5	6.0	5.5	5.5	5.0	4.5
7-13	6.0	6.0	6.0	6.0	5.0	4.5	4.5
7-17	6.5	6.5	6.5	6.5	5.5	5.5	5.0
7-20	7.5	7.5	7.0	7.0	6.0	5.5	5.0
7-26	8.0	8.0	7.5	6.5	5.5	5.0	5.0
7-27	9.5	9.5	9.0	7.5	6.0	5.0	5.0
8-2	11.0	10.5	10.5	10.5	9.5	6.5	5.5
8-4	12.5	12.5	12.5	12.0	10.0	8.0	7.0
8-8	16.5	16.0	15.0	15.0	15.0	10.0	8.5
8-10	18.0	18.0	17.5	15.0	14.5	13.5	9.5
8-14	19.5	19.5	19.0	17.5	16.0	14.0	9.5
8-17	17.7	17.0	17.0	16.0	14.0	11.0	8.5
8-25	16.5	16.0	15.5	15.5	12.0	11.0	9.5
8-28	15.5	15.5	15.5	15.0	13.5	12.5	9.5
9-5	16.0	15.5	15.0	15.0	14.0	13.5	9.5
9-15	15.5	15.0	14.5	14.5	14.5	14.0	7.0
11-10	7.5	6.5	5.5	5.0	4.5	4.5	4.5

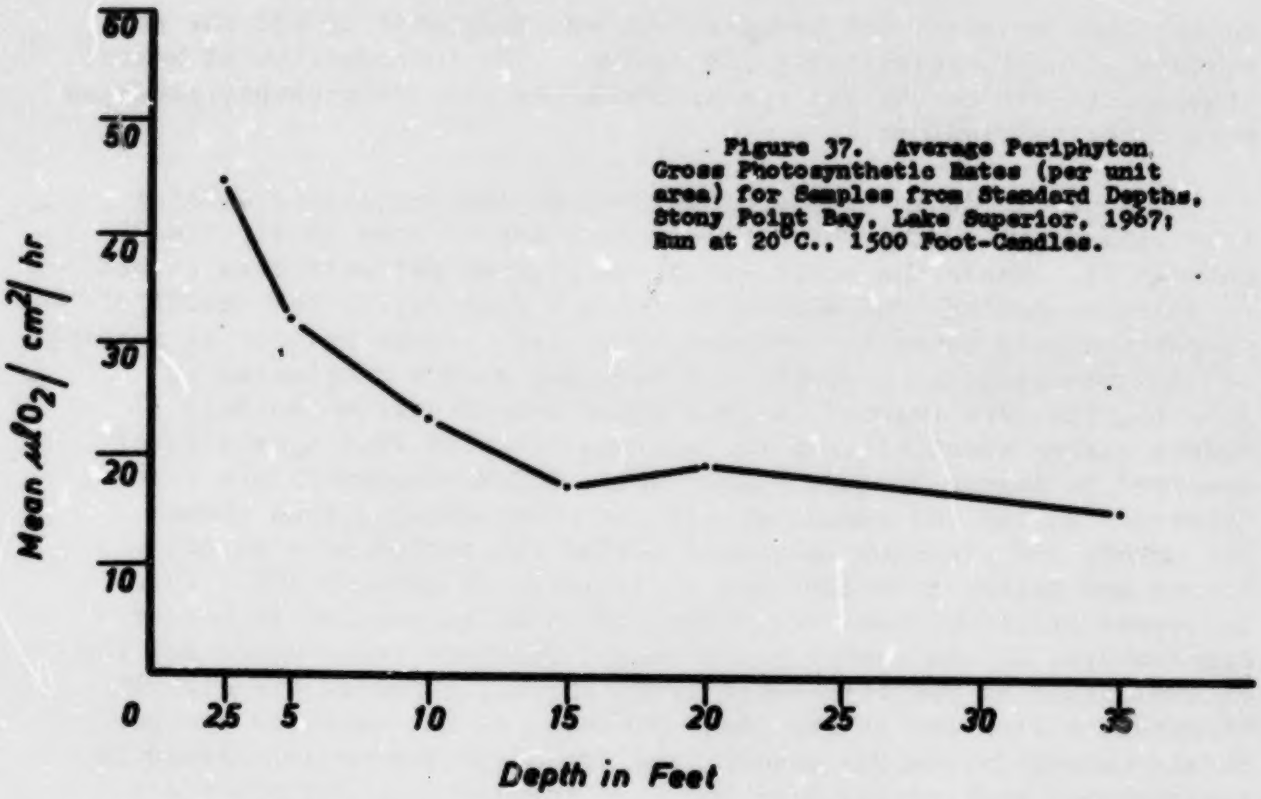

Figure 37. Average Periphyton Gross Photosynthetic Rates (per unit area) for Samples from Standard Depths, Stony Point Bay, Lake Superior, 1967; Run at 20°C., 1500 Foot-Candles.

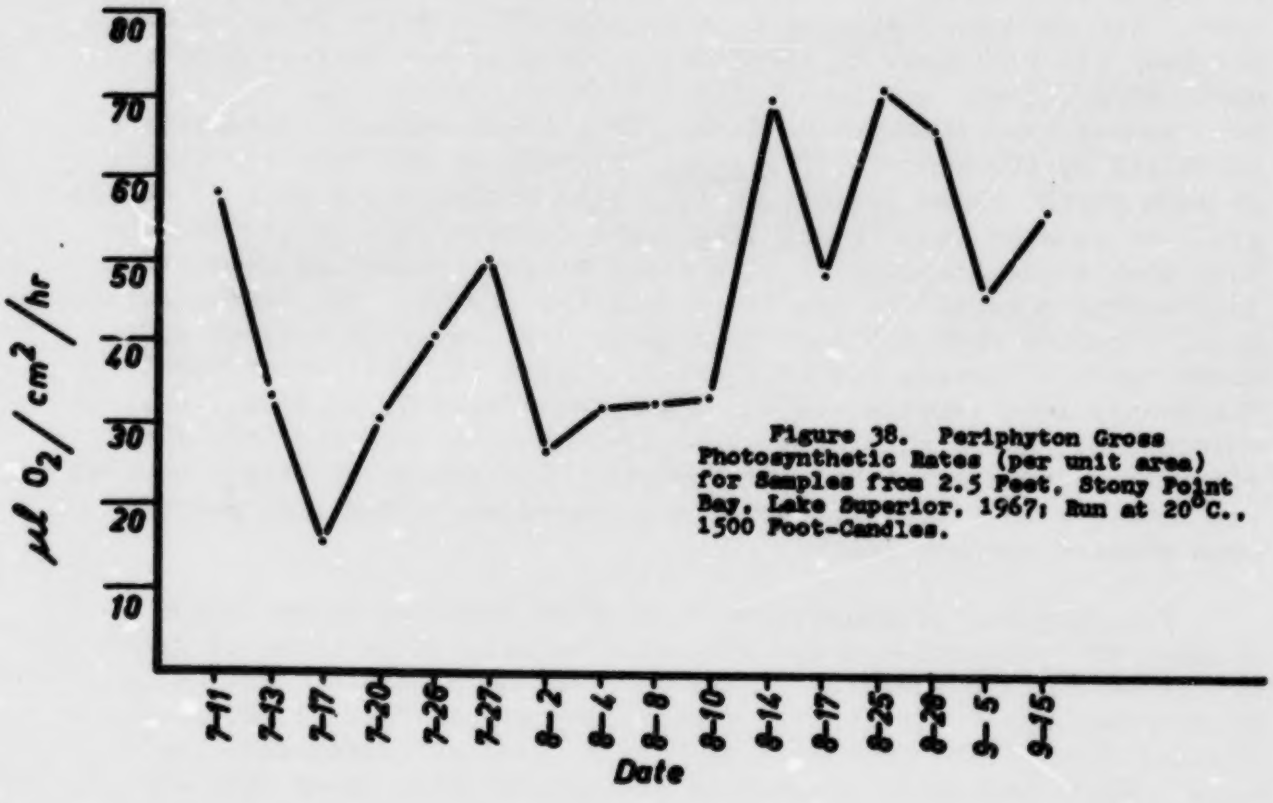

Figure 38. Periphyton Gross Photosynthetic Rates (per unit area) for Samples from 2.5 Feet, Stony Point Bay, Lake Superior, 1967; Run at 20°C., 1500 Foot-Candles.

rather than to speed the process. It was difficult to add the gas mixture without pressurizing the system. The introduction of normal atmospheric air to the gas spaces above the samples probably produced more accurate readings.

The variation in oxygen production by the periphyton samples from each depth during the entire summer may be seen in Figures 38 through 43. While the total amount of pigment per unit area seemed to decrease during the season at the 2.5 foot depth, the amount of oxygen produced tends to increase with time. After an initial reading of 58.4 microliters of oxygen per hour per square centimeter on July 11, the rate dropped to 15.6 microliters/hour/cm^2 on July 17 before rising eventually to the maximum value of 70.6 microliters/hour/cm^2 on August 25 (see Figure 38). Gross photosynthesis also increased during the summer at all the other depths, even though the counts and pigments increased during the period only at the twenty and thirty-five foot depths (Figures 39 through 43). This increased efficiency may have been due to an adaptation to warmer temperatures as the summer progressed. The test temperature for the determination of photosynthetic rate, 20° C., exceeded the highest temperature recorded in the bay. However, as the water in the bay became warmer during the summer, the organisms became accustomed to temperatures more nearly like the test temperature, and therefore performed the photosynthetic reactions more efficiently at that temperature.

When the production rate in terms of oxygen produced per hour per unit of ash-free dry weight is plotted against sampling depth (Figure 44), it is seen that photosynthetic efficiency depends on the depth from which the sample is taken, as well as on the time of year. The photosynthetic rate is highest (28.8 microliters of oxygen per hour per milligram of ash-free dry weight) for samples from a depth of 2.5 feet, and lowest (13.2 microliters/hour/mg. a.f.d.w.) for samples from thirty-five feet. This trend exactly opposes that exhibited by the amounts of pigment per unit of ash-free dry weight at each depth. When the amount of oxygen produced per unit of chlorophyll is plotted against sampling depth (Figure 45), it may be seen that the values are considerably lower at the twenty and thirty-five foot depths than at the shallower sampling depths. The rates remained quite constant from 2.5 feet to fifteen feet, averaging about 3000 microliters of oxygen per hour per milligram of total chlorophyll. The twenty foot samples evolved 2516 microliters O_2/hour/mg. total chlorophyll, while the thirty-five foot samples produced only 1566 microliters/hour/mg. total chlorophyll. The amount of oxygen evolved per hour per unit of chlorophyll a produced about the same pattern when plotted against depth.

For purposes of comparison with other reported assimilation values, the production rates were also calculated in terms of grams of carbon fixed per hour per gram of total chlorophyll. The value at 2.5 feet was 1.58; at five feet, 1.59: at ten feet, 1.70; at fifteen feet, 1.65; at twenty feet, 1.55; and at thirty-five feet, 0.84. These assimilation numbers are considerably lower than the

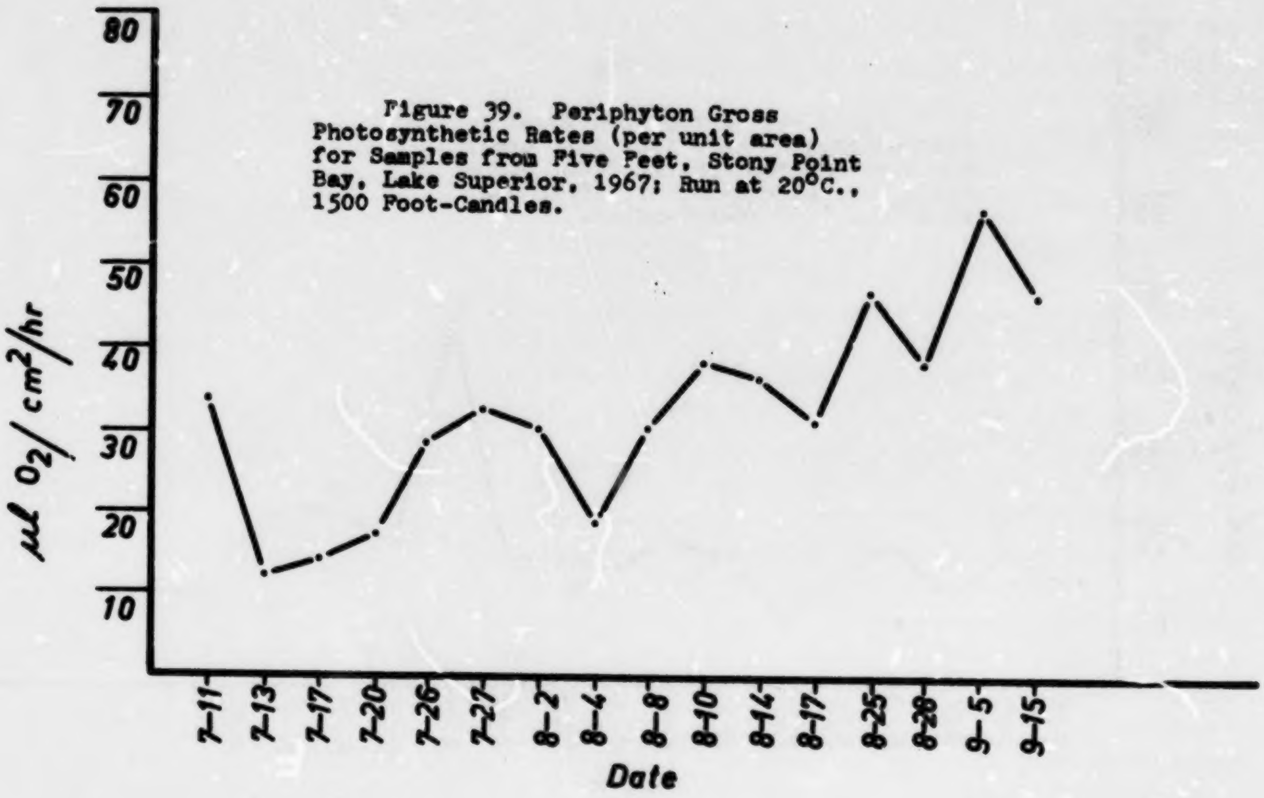
Figure 39. Periphyton Gross Photosynthetic Rates (per unit area) for Samples from Five Feet, Stony Point Bay, Lake Superior, 1967; Run at 20°C., 1500 Foot-Candles.

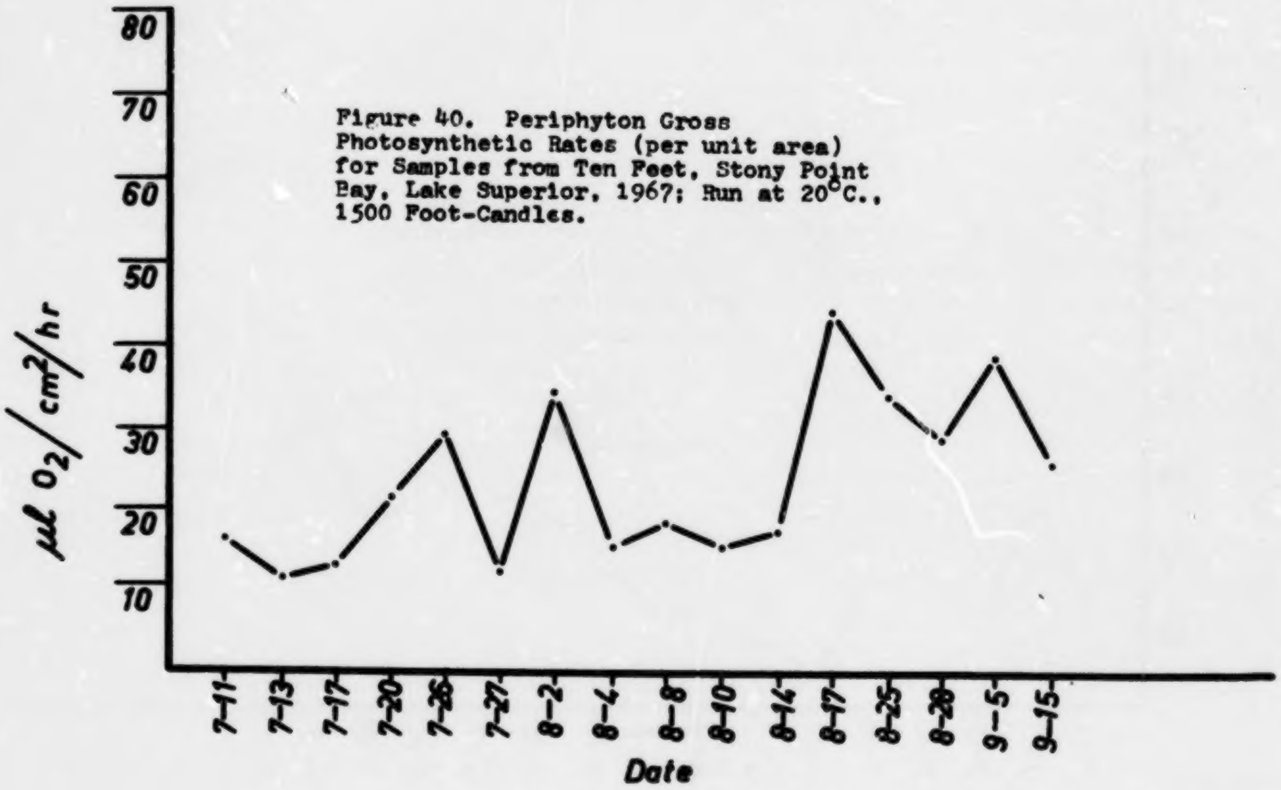
Figure 40. Periphyton Gross Photosynthetic Rates (per unit area) for Samples from Ten Feet, Stony Point Bay, Lake Superior, 1967; Run at 20°C., 1500 Foot-Candles.

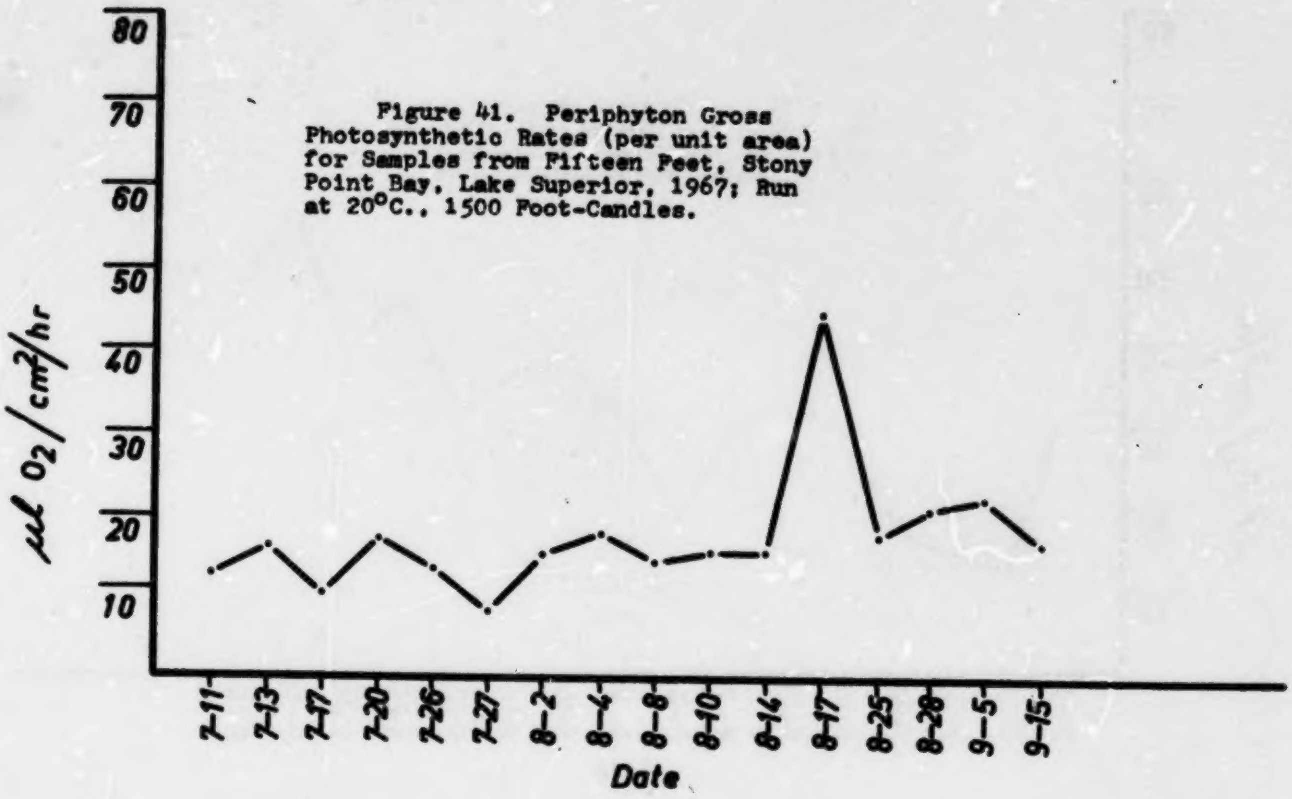

Figure 41. Periphyton Gross Photosynthetic Rates (per unit area) for Samples from Fifteen Feet, Stony Point Bay, Lake Superior, 1967; Run at 20°C., 1500 Foot-Candles.

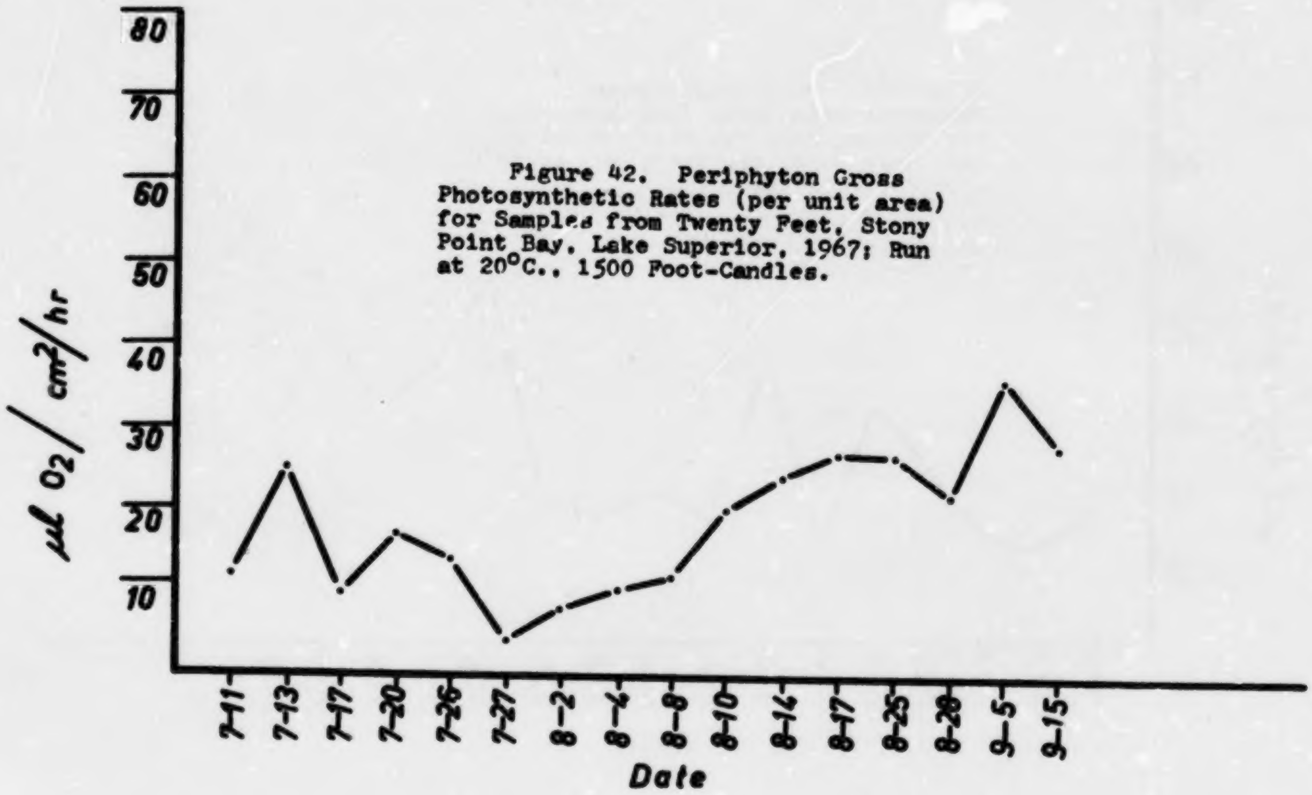

Figure 42. Periphyton Gross Photosynthetic Rates (per unit area) for Samples from Twenty Feet, Stony Point Bay, Lake Superior, 1967; Run at 20°C., 1500 Foot-Candles.

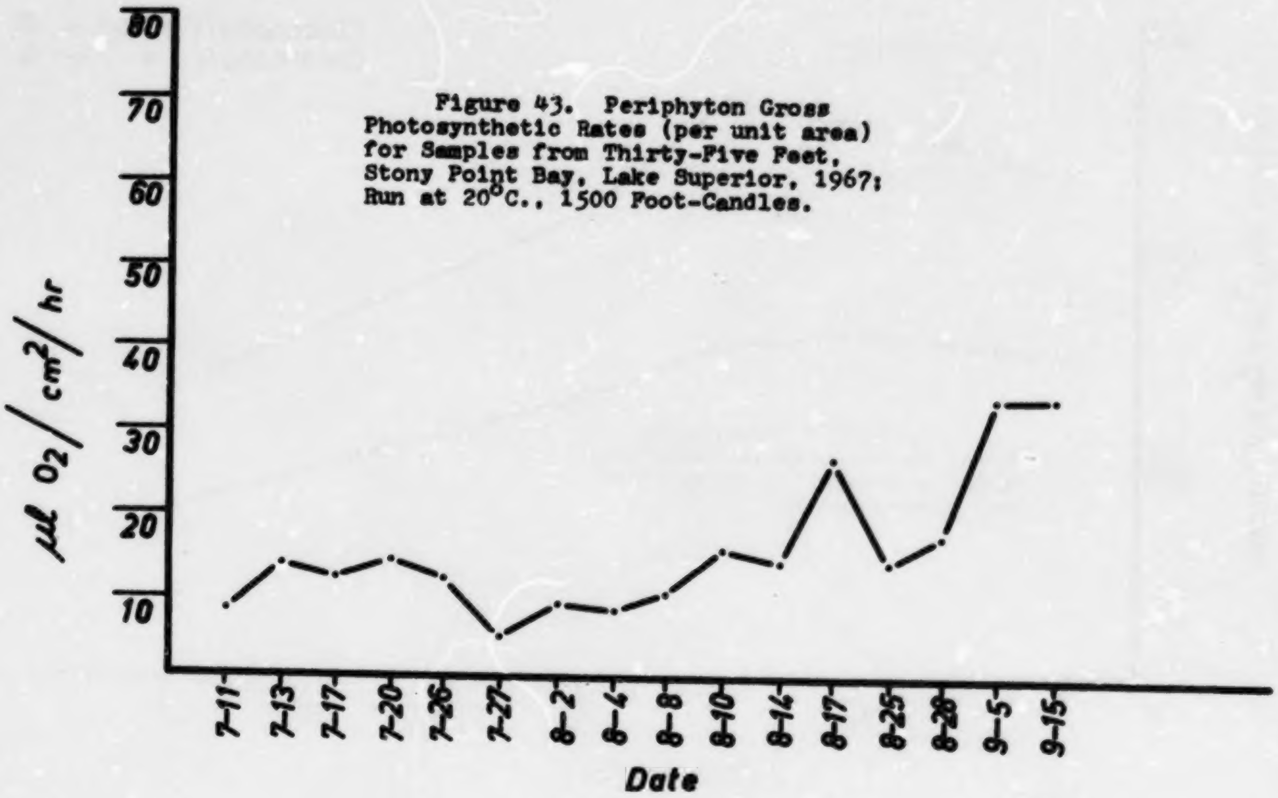

Figure 43. Periphyton Gross Photosynthetic Rates (per unit area) for Samples from Thirty-Five Feet, Stony Point Bay, Lake Superior, 1967; Run at 20°C., 1500 Foot-Candles.

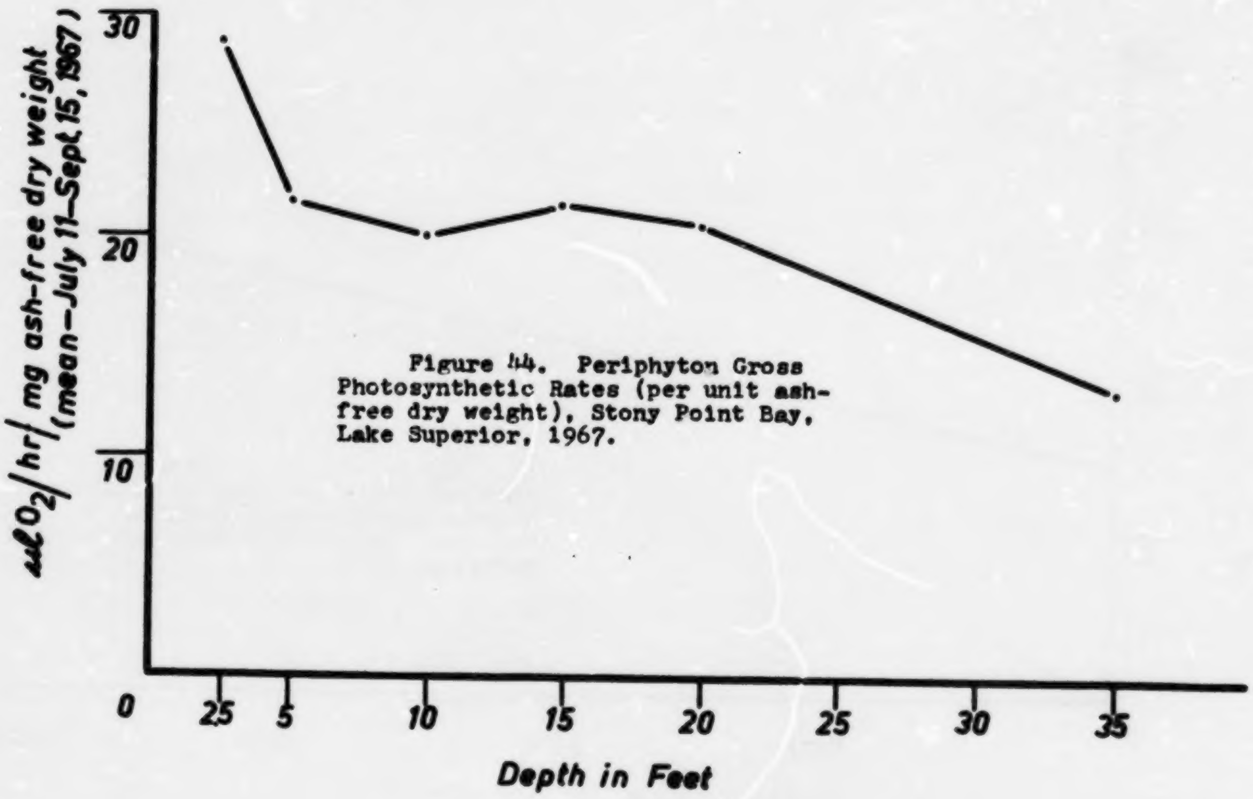

Figure 44. Periphyton Gross Photosynthetic Rates (per unit ash-free dry weight), Stony Point Bay, Lake Superior, 1967.

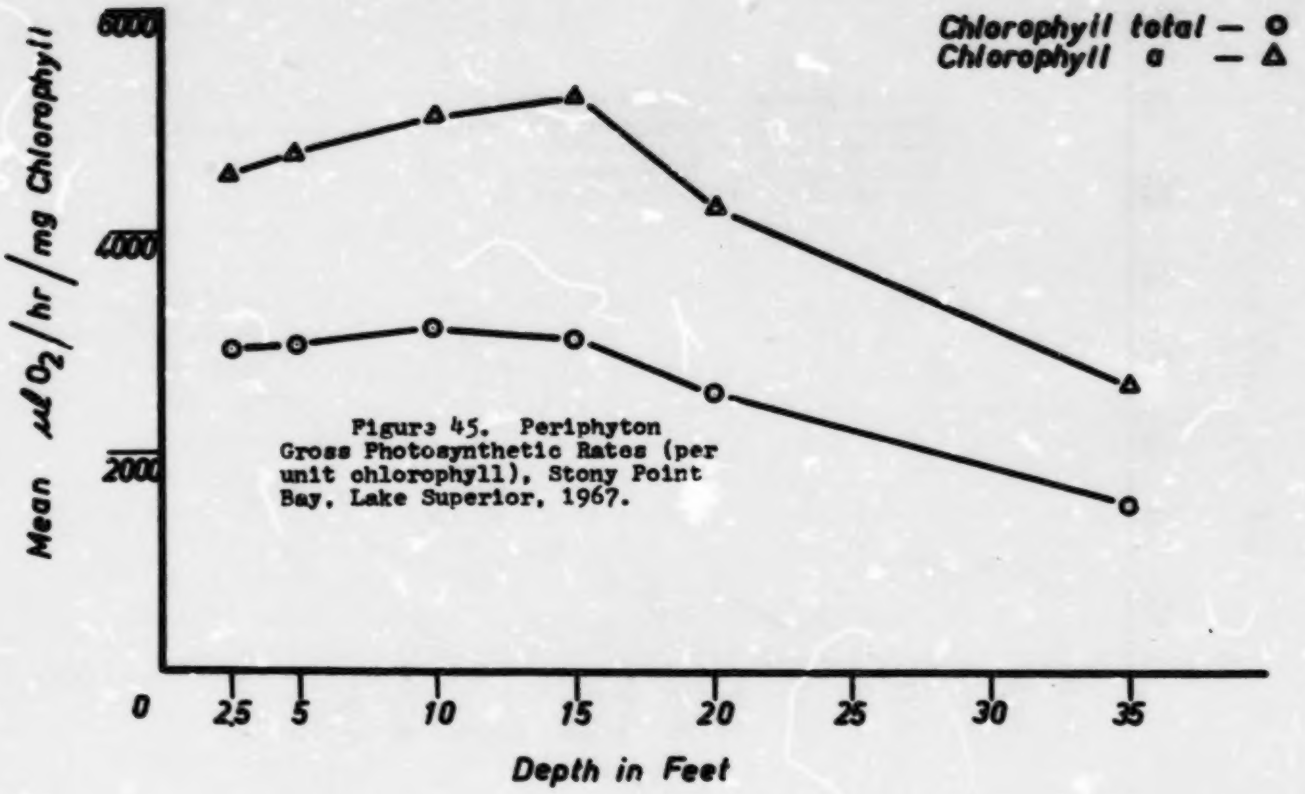

Figure 45. Periphyton Gross Photosynthetic Rates (per unit chlorophyll), Stony Point Bay, Lake Superior, 1967.

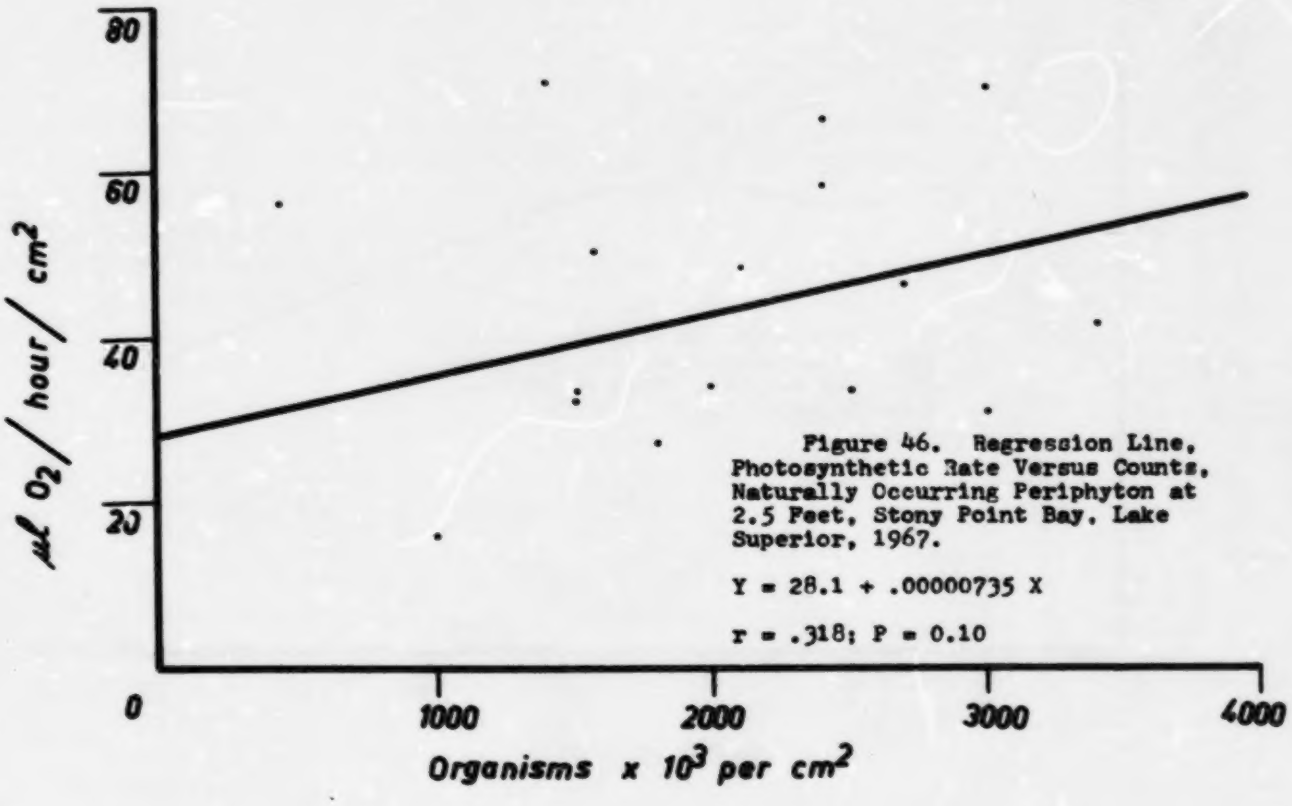

Figure 46. Regression Line, Photosynthetic Rate Versus Counts, Naturally Occurring Periphyton at 2.5 Feet, Stony Point Bay, Lake Superior, 1967.

$Y = 28.1 + .00000735\,X$

$r = .318;\ P = 0.10$

ones calculated for Stony Point Bay periphyton in 1966. The differences are probably due to the change in methodology employed in the determination of photosynthetic rate. The 1967 mean values represent many more analyses than were run in 1966, and are therefore considered to be more accurate.

The apparent decreased efficiency in photosynthesis with increasing depth may be due to adaptation to both temperature and light intensity. It has been shown that temperature decreased with depth; therefore, the organisms grown in the shallow, warmer water would be more apt to function at a more rapid rate at the test temperature (20° C.) than those grown in deep, colder water. Average light intensity has also been shown to decrease as depth increases in the bay. The average intensities at fifteen, twenty and thirty-five feet were lower than in the standard test procedure; the samples from these depths, then, would not be as accustomed to the test intensity as those taken from the shallow depths. In order to further determine the magnitude of variablility in the relationship between pigment concentrations and photosynthetic rate, a correlation coefficient was calculated for these two parameters of productivity. The correlation coefficient for the combined data for all depths was 0.573 (P=0.001), indicating a rather weak positive correlation.

Correlation coefficients were also calculated for total counts and photosynthetic rate for each sampling depth, to test the seasonal variation in this relationship. Regression lines were also constructed as a means for estimating production rates from numbers of organisms. The regression lines, correlation coefficients (r), and probability values (P) are shown in Figures 46 through 51. The correlations were positive at all depths, but were rather poor except for the thirty-five foot samples. The data for the fifteen foot samples produced the lowest coefficient (r=0.249, P=0.10); the two measurements correlated best at thirty-five feet (r=0.844, P=0.001). Generally speaking, one could not expect very accurate predictions of production rates based on enumeration of organisms, even when the sampling depth is known. If the depth were not known, such a prediction would not be at all advisable. The relationship between pigments and counts, and between photosynthesis and counts are apparently variable with respect to time. There are obvious differences in the relationships in terms of the depth at which the organisms grew. These statements should not imply that the differences occur randomly; work performed in 1968 has shown that these differences may be ascribed to environmental factors. As will be seen in a following section, measurements made under standard laboratory conditions may be adjusted to account for existing environmental conditions at the time of sampling.

The 1967 photosynthesis data are presented in several ways in Table XI. The average net photosynthetic rate for periphyton samples from all depths was 17.3 microliters of oxygen evolved per hour per square centimeter of rock surface. The ratio of gross photosynthesis to respiration ranged from 2.96 for samples from a depth of fifteen feet to 3.46 for samples from five feet, and averaged 3.17. The photosynthetic rates were converted to net daily production values,

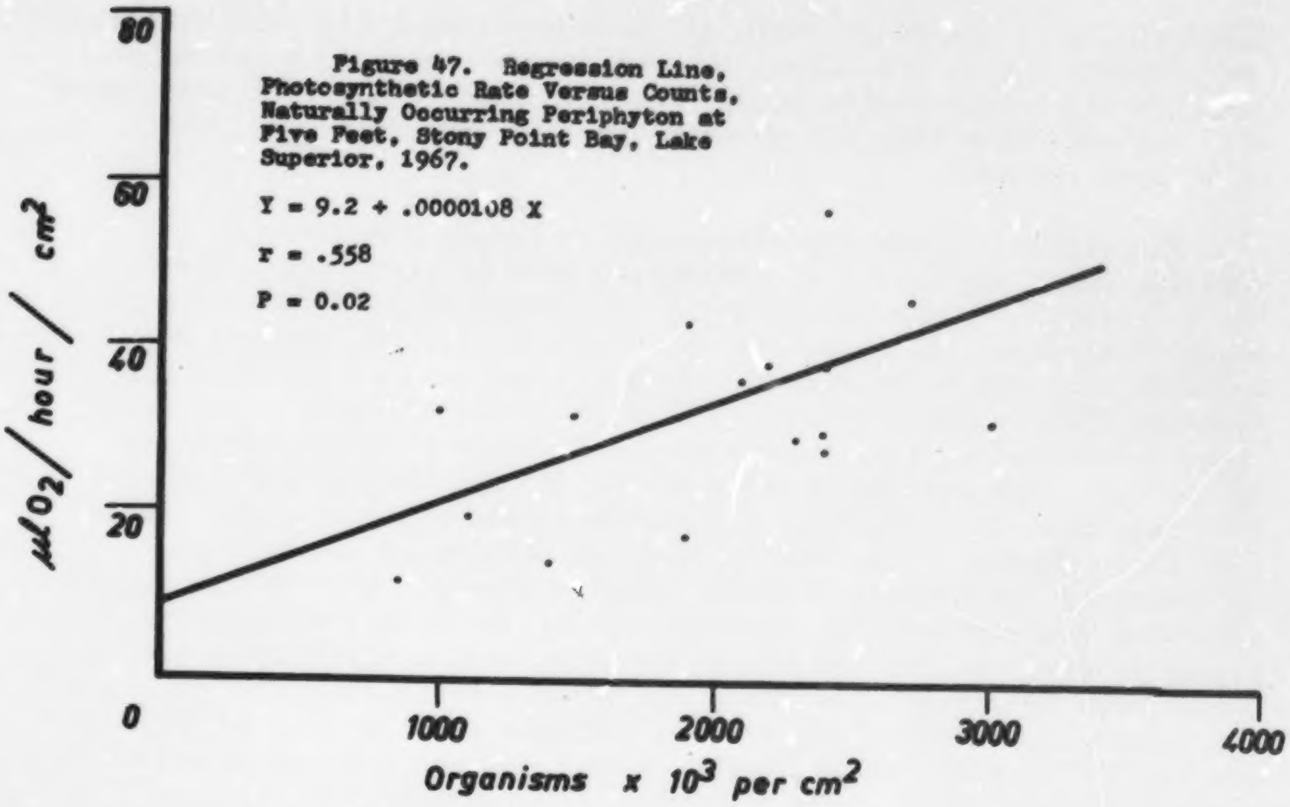

Figure 47. Regression Line, Photosynthetic Rate Versus Counts, Naturally Occurring Periphyton at Five Feet, Stony Point Bay, Lake Superior, 1967.

$Y = 9.2 + .0000108 X$

$r = .558$

$P = 0.02$

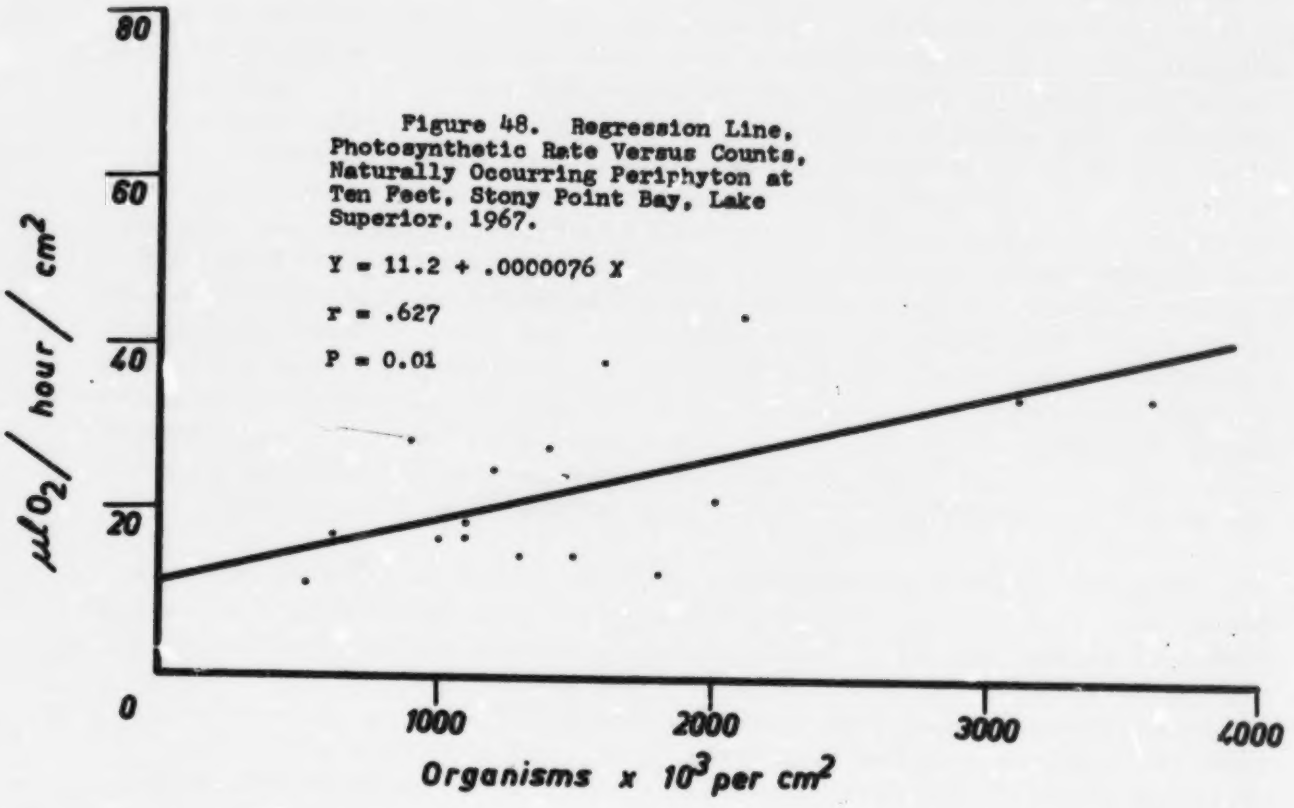

Figure 48. Regression Line, Photosynthetic Rate Versus Counts, Naturally Occurring Periphyton at Ten Feet, Stony Point Bay, Lake Superior, 1967.

$Y = 11.2 + .0000076 X$

$r = .627$

$P = 0.01$

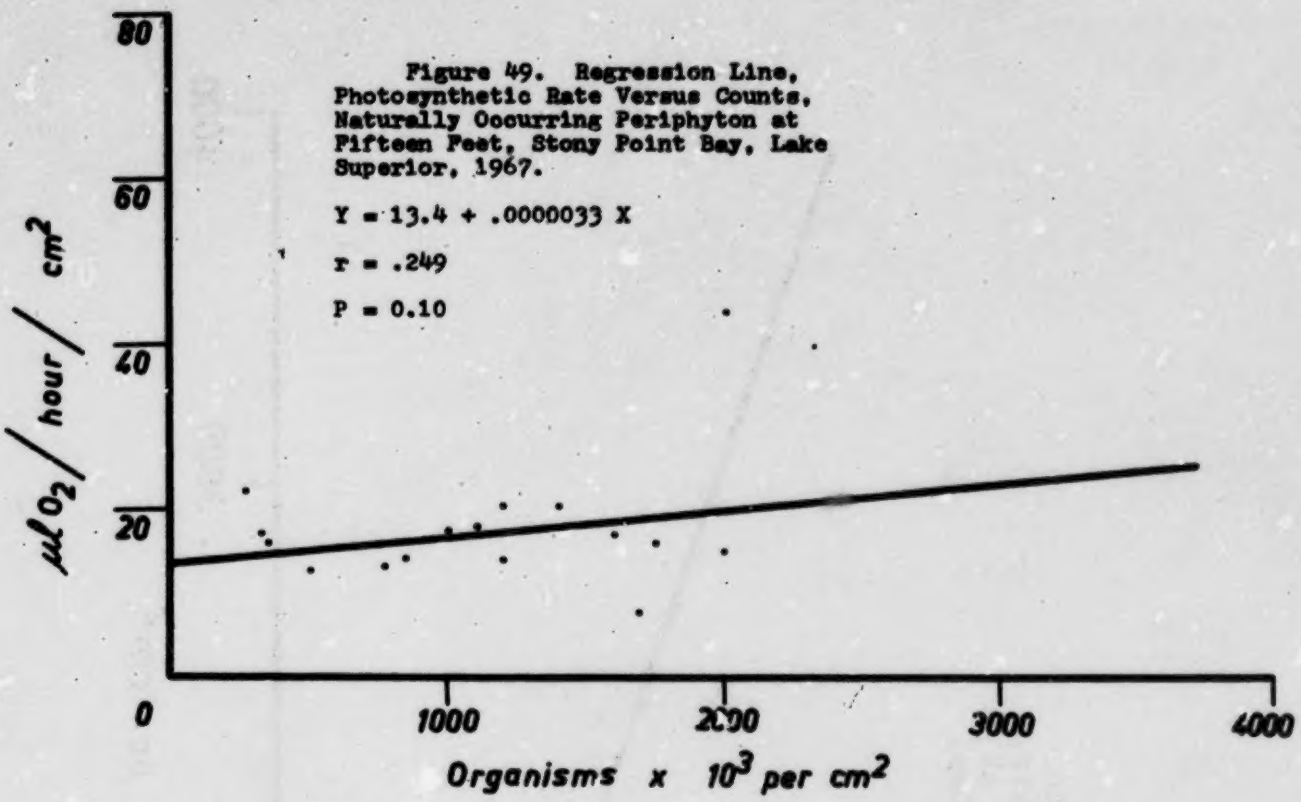

Figure 49. Regression Line, Photosynthetic Rate Versus Counts, Naturally Occurring Periphyton at Fifteen Feet, Stony Point Bay, Lake Superior, 1967.

$Y = 13.4 + .0000033 X$

$r = .249$

$P = 0.10$

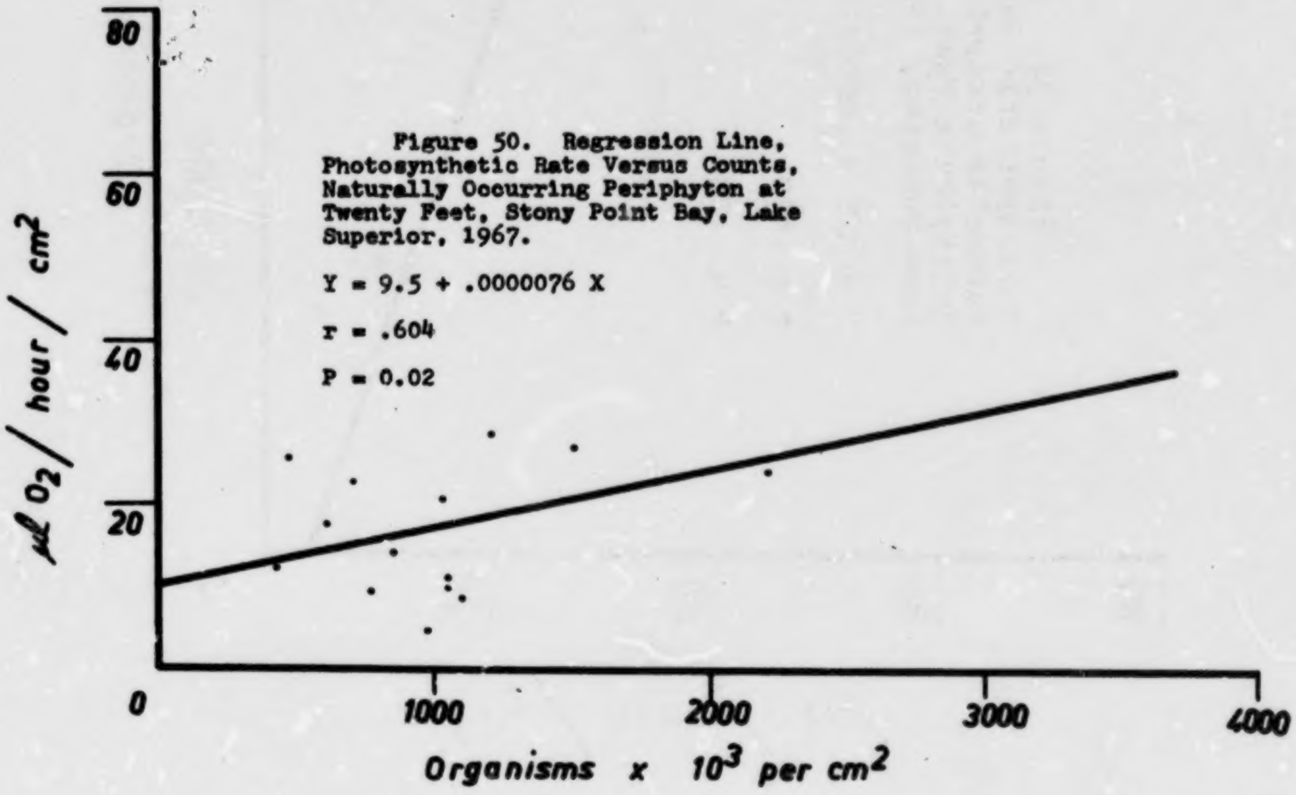

Figure 50. Regression Line, Photosynthetic Rate Versus Counts, Naturally Occurring Periphyton at Twenty Feet, Stony Point Bay, Lake Superior, 1967.

$Y = 9.5 + .0000076 X$

$r = .604$

$P = 0.02$

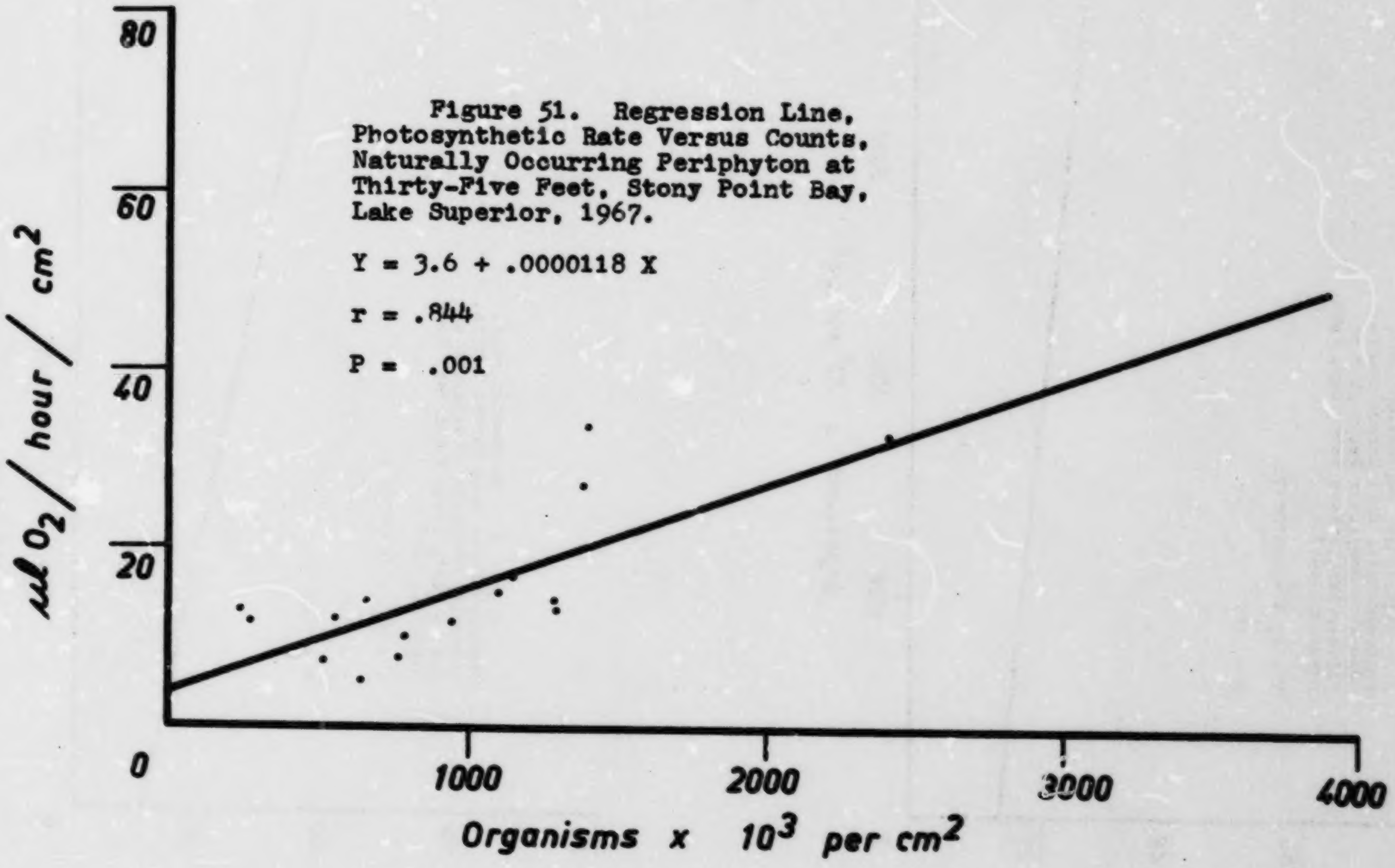

Figure 51. Regression Line, Photosynthetic Rate Versus Counts, Naturally Occurring Periphyton at Thirty-Five Feet, Stony Point Bay, Lake Superior, 1967.

$Y = 3.6 + .0000118\ X$

$r = .844$

$P = .001$

TABLE XI

PHOTOSYNTHESIS DATA FOR PERIPHYTON SAMPLED AT DIFFERENT DEPTHS, STONY POINT BAY, 1967 RUN AT 20°C, 1500 FOOT-CANDLES

	Sampling depth in feet						
	2.5	5	10	15	20	35	Mean
Gross photosynthesis							
ul $O_2/cm^2/hr$	+44.6	+31.8	+23.0	+17.2	+19.2	+15.3	+25.2
Respiration							
ul $O_2/cm^2/hr$	-13.9	-9.2	-7.6	-5.8	-5.7	-5.1	-7.9
Net photosynthesis							
ul $O_2/cm^2/hr$	+30.7	+22.6	+15.4	+11.4	+13.5	+10.2	+17.3
P/R	3.21	3.46	3.03	2.96	3.36	3.00	3.17
Net production							
Grams carbon fixed per M^2 per day	1.79	1.36	0.87	0.63	0.81	0.57	1.01
Grams (as Glucose) per M^2 per day	5.96	4.53	2.90	2.10	2.70	1.90	3.35

as carbon fixed per unit area and as glucose produced per unit area. Net production in terms of carbon fixed varied from 0.57 grams per square meter per day at thirty-five feet to 1.79 grams per square meter per day at 2.5 feet; the average value was 1.01. The mean production rate (as glucose) for all depths was 3.35 grams per square meter per day. For the purpose of calculating mean production rates for the entire bay, it was decided that the data for each of the sampling depths would apply to a strip of the bay as wide as half the distance to the next shallower sampling point plus half the distance to the next deeper sampling point. Since the sampling area was pie-shaped, and since the sampling points were progressively further apart toward the deeper water (see Figure 2), the area corresponding to each sampling depth was virtually the same size; therefore, each production value was given equal weight in the determination of the mean. All of the net photosynthesis data was calculated on the basis of a fifteen-hour day, and takes into account daytime and nighttime respiration.

The production rates calculated for Stony Point Bay in 1967 may be compared with those reported for other periphyton communities and certain phytoplankton communities. In making such comparisons it is realized that the methodology varies in each investigation and that differences or similarities may often be attributed to methodology. The average rate of carbon fixation by Stony Point Bay periphyton, 1.01 grams/M^2/day, compares rather well with the value reported for the periphyton of the Logan River in Utah (0.6 grams/M^2/day) by McConnell and Sigler (1959). Kobayasi (1961) found a production rate of 0.33 grams of carbon fixed/M^2/day in the natural epilithic periphyton of the Arakawa River in Japan. In both of these investigations, the light and dark bottle oxygen technique was used, possibly producing lower results than would be obtained with a manometric method. In addition, incubation of samples by Kobayasi and by McConnell and Sigler was accomplished by submerging the bottles in water at approximately 11° C., considerably lower than the test temperature (20° C.) used in the Stony Point Bay study. On this basis, one might logically invoke Van't Hoff's law, namely, that the reaction rate doubles for each 10° C. increase in temperature, and raise the Logan River value to 1.2 and the Arakawa River value to 0.66. The nutrient concentrations in the two rivers were quite low, as are those found in Lake Superior. Wetzel (1963) has reported a mean production value of 0.73 grams of carbon fixed/M^2/day for the periphyton of Borax Lake, in California. The actual production rates in the four periphyton communities compared above are probably very similar.

Carbon fixation rates for communities other than periphyton are quite variable and include a wide range of reported values. For instance, Odum (1957) has shown the production rates in eleven Florida springs, including the plankton and the periphyton, to range from 0.17 to 18.1 grams of carbon fixed/M^2/day. A value of 0.49 grams of carbon fixed/M^2/day for the phytoplankton of Weber Lake, in Wisconsin, has been reported by Manning and Juday (1941). Hogetsu and Ichimura (1954) determined the mean production rate for the phytoplankton of Japan's Lake Suwa to be 0.44 grams of carbon fixed/M^2/day. Data provided by Olson and Putnam (1961) show that the phytoplankton of Lake Superior at Larsmont, not far from Stony Point Bay, fix an average of 0.17 grams of carbon per square meter per day during the summer months. Based on this result, it is concluded that the periphyton of Stony Point Bay can produce five to six times as much organic matter as the phytoplankton in the area within one-half mile of shore.

In 1967, the periphyton of Stony Point Bay contained 0.097 grams of chlorophyll per square meter of rock surface. This value is lower than the mean yearly chlorophyll concentration in the periphyton of the Logan River (0.30 grams/M^2) as measured by McConnell and Sigler (1959), and somewhat higher than the 0.040 grams/M^2 reported by Kobayasi (1961) for the Arakawa River periphyton. The periphyton growing in the Arakawa River at the time of Kobayasi's investigation was made up primarily of diatoms. Wetzel (1963) found the mean concentration of chlorophyll in the periphyton of Borax Lake to be 0.32 grams/M^2. Values ranging from 0.43 to 2.01 grams of chlorophyll/M^2 in laboratory streams have been recorded as the communities changed from those dominated by diatoms to those dominated by Phormidium (McIntire and Phinney, 1965).

According to Odum (1959), Gessner has stated that the chlorophyll of diverse communities develops in very similar amounts on a square meter basis, thus providing an example of "community homeostasis." In light of this contention, it is interesting to compare the chlorophyll concentration of Stony Point Bay periphyton (0.097 grams per M^2) with the concentrations in phytoplankton communities. The concentration of chlorophyll in Lake Superior phytoplankton at the Larsmont station during the summer of 1961 averaged 0.017 grams/M^2 (calculated from data presented by Putnam and Olson, 1961). According to Hogetsu and Ichimura (1954), the phytoplankton of Lake Suwa also supported less chlorophyll (0.066 grams per M^2) than Stony Point Bay periphyton. However, a much higher value, 0.27 grams/M^2, has been reported for the Gerlache Straits of Antarctica by Burkholder and Sieburth (1961).

Very little information is available regarding assimilation values for periphyton communities. The mean assimilation value for Stony Point Bay periphyton was 1.4 grams of carbon fixed per hour per gram of chlorophyll, according to the 1967 data. This figure compares well with those reported for the epilithic periphyton of the Arakawa River by Kobayasi (1961). When measured at a light intensity of 30,000 lux (2778 foot-candles), the organisms fixed 0.75 grams of carbon/hour/gram of chlorophyll at 12° C. and 1.9 grams of carbon/hour/gram of chlorophyll at 26° C. McConnell and Sigler (1959) report an assimilation value of 0.75 grams of carbon fixed/hour/gram of chlorophyll in the periphyton of the Logan River. These figures agree very well with the assimilation value calculated for Stony Point Bay periphyton under the test conditions. Since certain accessory pigments have been shown to be active in photosynthesis, an assimilation value based on total pigments should be calculated for all communities studied, so that the photosynthetic efficiencies of diverse communities can be more accurately compared in the future. For the periphyton of Stony Point Bay this value would be 1.12 grams of carbon fixed/hour/gram of total pigment.

It is difficult to compare the weights of Stony Point Bay periphyton with weights reported for other periphyton communities because most other investigations have involved the use of suspended glass slides for the accumulation of organisms. Periphytic communities developing on these slides do not contain the significant amounts of sand and clay that are found in natural communities. The periphyton developing on glass plates in several freshwater lakes in Washington produce an average dry weight of only 0.15 grams per square meter, compared to 156 grams per square meter for Stony Point Bay periphyton. Corresponding organic weights were 0.015 and 12 grams per square meter. The organic weight of the material in the Washington lakes was 34 per cent of the dry weight, while the organic weight of the Stony Point Bay periphyton was only 7.7 per cent of the dry weight; this discrepancy emphasizes the fact that natural communities contain large amounts of sand. Newcombe (1950) reports that the periphyton developing on glass slides in Sodon Lake, Michigan, produced dry weights ranging from 0.5 to 2.0 grams/M^2 and ash-free dry weights varying between 0.16 and 0.95 grams/M^2 (32 to 49 per cent). The average dry weight of the natural epilithic community in the Logan River was shown to be 25 grams/M^2 (McConnell and Sigler, 1959), while the periphyton community of Sedlice Reservoir, in Czechoslovakia, weighed 15.9 grams/M^2 (Sladecek and Sladeckova, 1963). According to Atkins and Parke (1951), the chlorophyll of many marine algae makes up from 2.3 to 2.9 per cent of the organic weight. The chlorophyll of Stony Point Bay periphyton accounts for only 0.8 per cent of the organic weight.

Considering the data as a whole, the periphyton of Stony Point Bay as measured by several parameters seems to be indicative of an oligotrophic situation. The pigment ratios indicate a community dominated by diatoms. The measures of biomass show that the growths are of average magnitude when compared with the communities of other bodies of relatively clean water. The production rate in the bay, based on photosynthetic activity, is also similar to the rates exhibited by the periphyton of mountain streams, springs and other cold lakes.

Periphyton Occurring as Regrowth, Stony Point Bay

From July 31 to November 9, 1967, a study to determine the rate of establishment of periphyton organisms on denuded, autoclaved rocks was conducted in Stony Point Bay. In the course of the study, eighty-four rocks were recovered from the three stations where they had been placed on July 31. These stations were at depths of ten, twenty and thirty-five feet. Selected "incubation times" ranged from eight hours to 101 days. On the final sampling day, November 9, samples were collected only at the thirty-five foot depth, because the marker buoys for the other two stations had been dislodged by a storm.

The amounts of chlorophylls a, b, and c per unit area of rock surface at each sampling time are presented in Figures 52 through 54. In general, the chlorophyll concentrations increased continually during the study period, rising to a maximum at all three depths on September 15, the last day on which all depths were sampled. On any given day, the amount of chlorophyll per unit area was found to be about equal at the three depths. At the ten foot depth, chlorophyll a increased from 0.004 milligrams per 100 square centimeters to 0.165 milligrams per 100 square centimeters during the forty-six day period. The chlorophyll a concentration at twenty feet began at 0.004 mg /100 cm^2 and rose to 0.213 mg./100 cm^2, while at thirty-five feet, the concentration increased from 0.003 mg./100 cm^2 to 0.185 mg./100 cm^2. The concentration of chlorophyll a at the thirty-five foot depth had dropped to 0.108 mg. /100 cm^2 by November 9 (101 days). The only other depression occurred on August 28, and was apparent in both the ten and thirty-five foot samples.

Chlorophyll c, chlorophyll b, and non-astacin carotenoids were present in about the same relative amounts as in the naturally occurring periphyton of Stony Point Bay, indicating that the same types of organisms were present. All of the pigment groups increased with time except the astacin carotenoids, which varied between 0.002 and 0.015 MSPU/100 cm^2 at all three depths and were as low on September 15 as they were on August 4 (0.004 MSPU/100 cm^2). The varying astacin carotenoid concentrations are probably indicative of the presence of inconsistent numbers of Cladocerans in association with the attached algae. The ratio of chlorophyll c to chlorophyll a varied widely during the sampling period, occasionally exceeding unity when the total concentrations were very low. On the other hand, the increase in the concentration of non-astacin carotenoids during the summer closely paralleled that of the chlorophyll a concentration; the ratio of non-astacin carotenoids to chlorophyll a did not vary significantly from 0.360 at ten feet, 0.312 at twenty feet, and 0.302 at thirty-five feet. Chlorophyll b concentrations remained quite low throughout the period, reaching a maximum of 0.035 mg. per 100 cm^2 at the twenty foot depth on August 28. Since the chlorophyll b concentration also peaked on the same date at the other sampling depths, it appears that the relative number of green algae in the regrowth material reached a maximum on that date.

When the total chlorophyll concentrations obtained on the last regular day of sampling (September 15) are divided by their "incubation" time (forty-six days), daily production rates are produced. The daily rates for accumulation of chlorophyll at ten, twenty and thirty-five feet are 0.00046, 0.00069, and 0.00056 grams per square meter per day. No other investigations have been encountered in which the measurement of chlorophyll has been employed to determine the rate of periphyton accumulation on a natural substrate in the lentic situation. However, while observing the growth of periphyton on concrete cylinders in a river, Waters (1962) found that three to eight weeks were required for the chlorophyll concentration to reach a maximum level. Past that point, seasonal variations were shown.

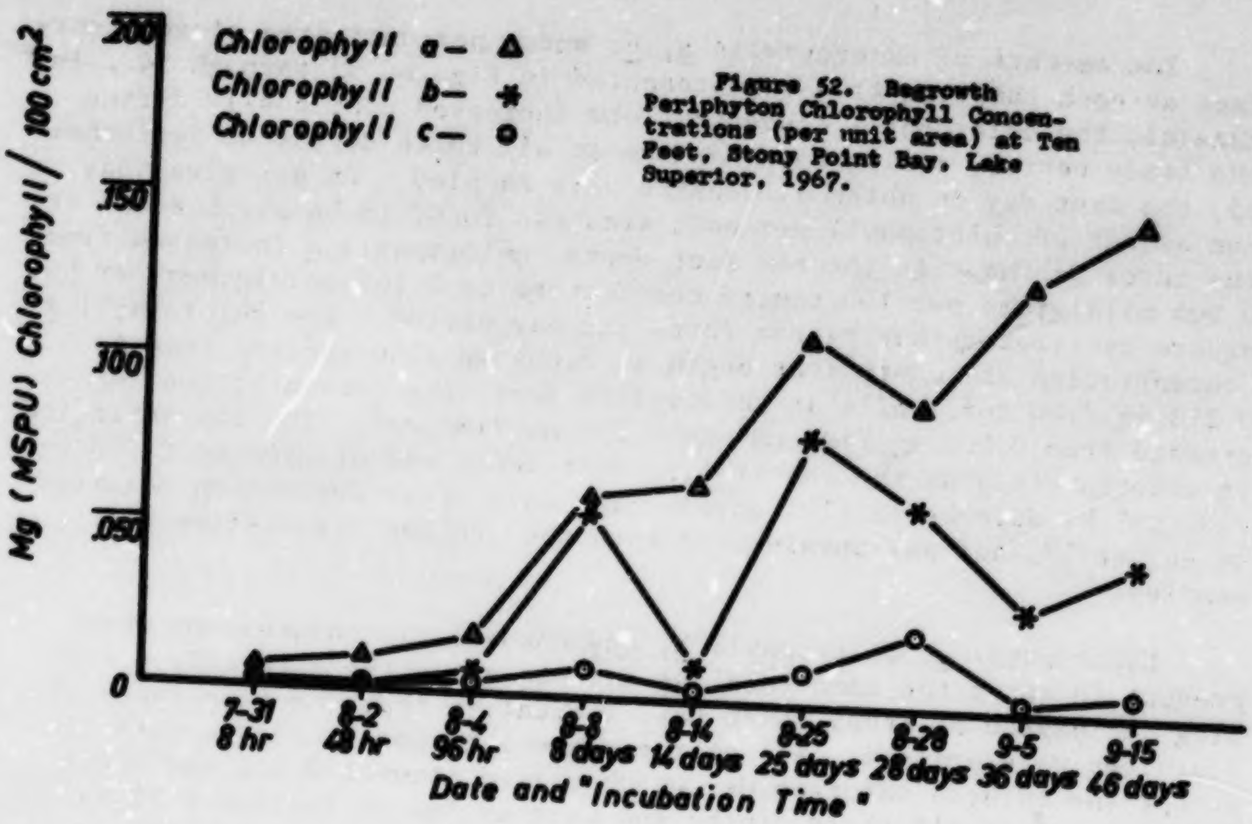

Figure 52. Regrowth Periphyton Chlorophyll Concentrations (per unit area) at Ten Feet, Stony Point Bay, Lake Superior, 1967.

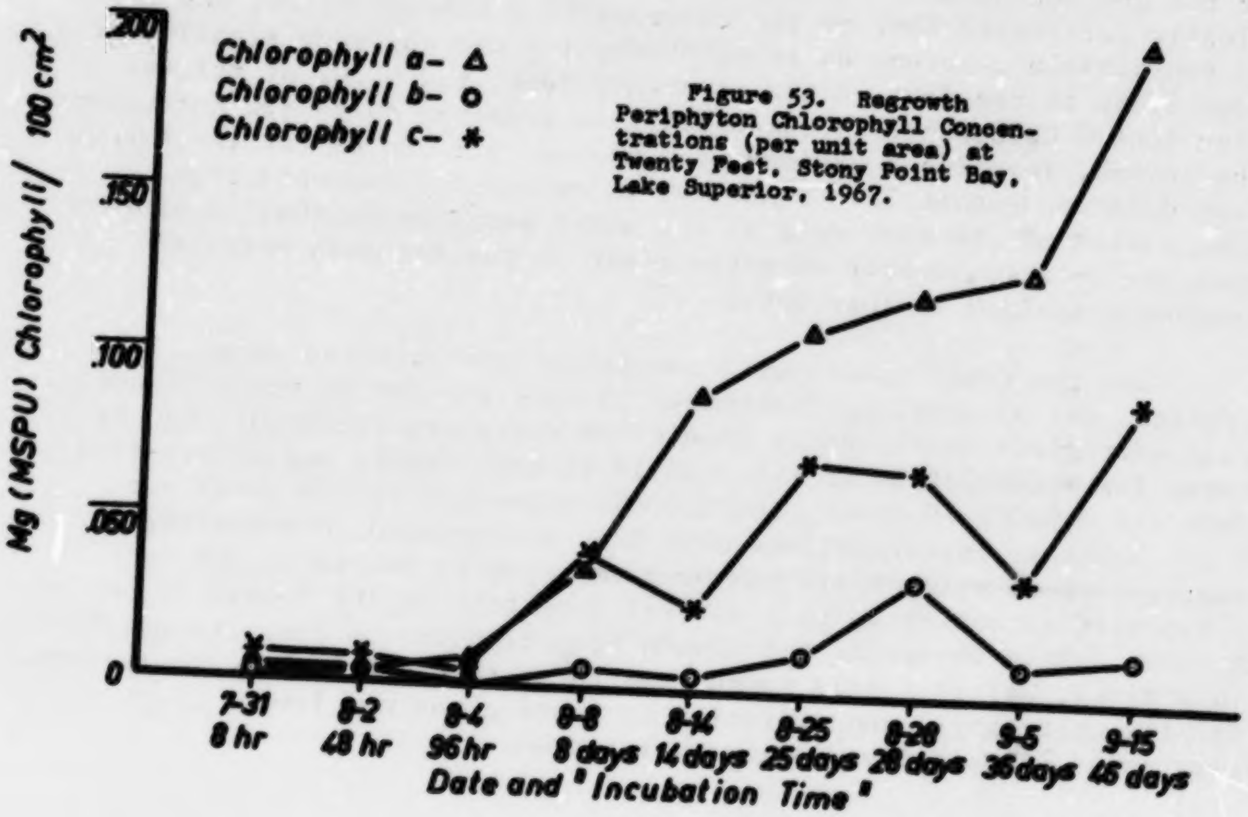

Figure 53. Regrowth Periphyton Chlorophyll Concentrations (per unit area) at Twenty Feet, Stony Point Bay, Lake Superior, 1967.

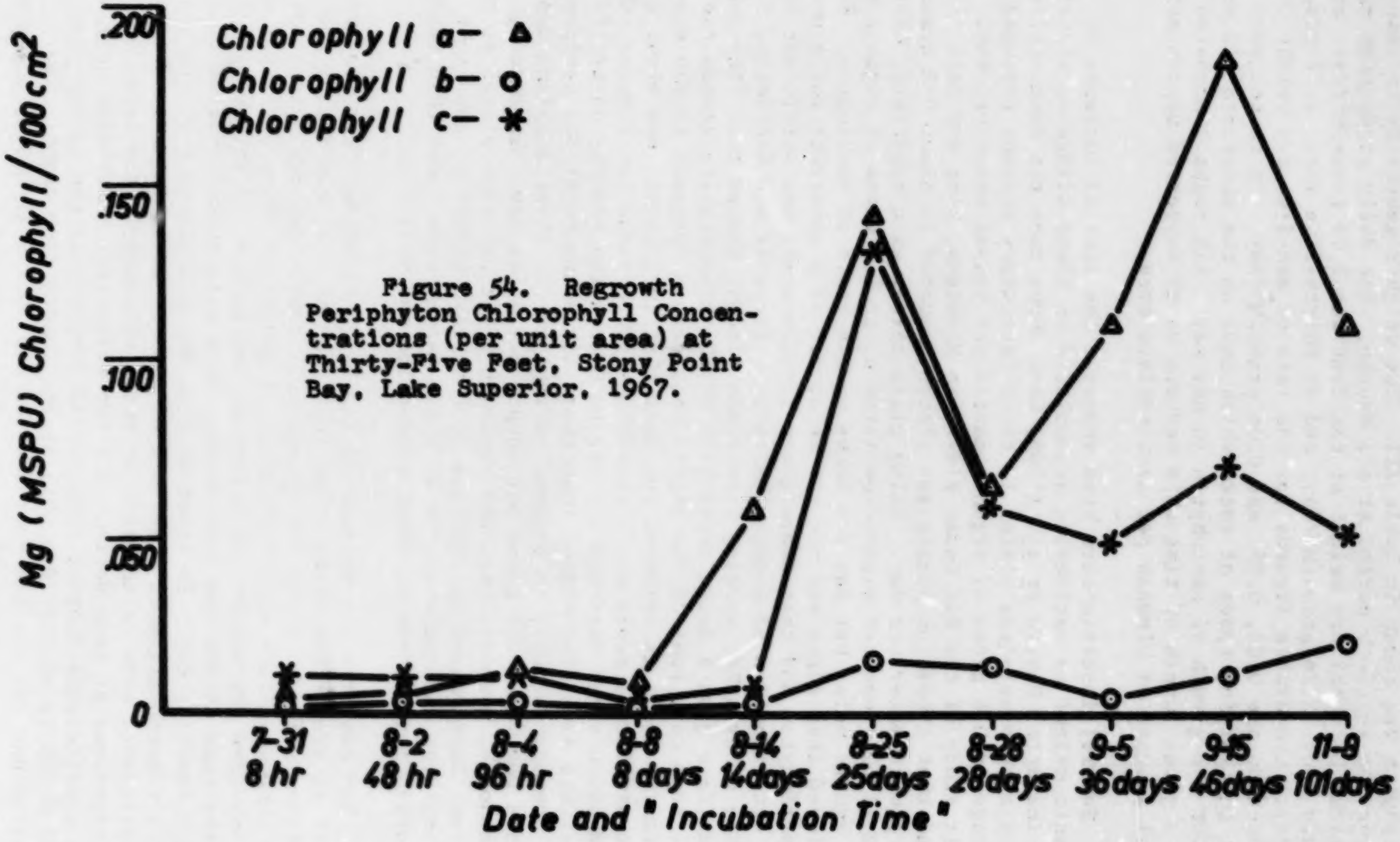

Figure 54. Regrowth Periphyton Chlorophyll Concentrations (per unit area) at Thirty-Five Feet, Stony Point Bay, Lake Superior, 1967.

The total dry weights and ash-free dry weights of the regrowth periphyton are shown in Table XII. The weights generally increased during the regrowth period at all depths. The daily production rate in terms of total dry weight at ten feet was 5.76 grams/M^2/day; at twenty feet, 2.26 grams/M^2/day; and at thirty-five feet, 2.77 grams/M^2/day. Comparable figures for the rate of ash-free dry weight production are 0.09, 0.05, and 0.06 grams/M^2/day. It is believed that the varying types of rocks which made up the substrata did not affect the growth of periphyton in any way. All rocks "incubated" for a given length of time at a certain depth supported approximately equal amounts of biomass per unit surface area.

Several investigators have reported the rate of increase in organic weight as periphyton accumulated on glass slides or plates. For instance, Kevern *et al*. (1966) have shown that the communities colonizing plexiglass plates in their laboratory streams produced an average of 0.6 grams of organic matter per square meter per day. In their study of the Red Cedar River, in Michigan, King and Ball (1966) found that growth on plexiglass plates amounted to about 0.3 grams per square meter per day. Using glass slides as a substrate, Castenholz (1960) reported production rates up to 0.5 grams of organic weight per square meter per day for lakes in the state of Washington. He believed that glass was not too selective as a substrate for growth of periphyton and that submergence for two weeks was sufficient for the determination of production rates. Foerster and Schlicting (1965), on the other hand, working with glass slides, stated that "the artificial surface gave a false impression of the productivity trends and indicated only some of the significant genera present in the ecosystem." Thus, in spite of the fact that in general, one might expect that artificial media would result in lower production figures, the production rates reported for stream periphyton growing on artificial substrata are often higher than those for Stony Point Bay periphyton. The average increase in organic weight at the three sampling depths in the bay was 0.066 grams per square meter per day. It must be remembered, however, that the regrowth substrata were placed at depths of ten, twenty, and thirty-five feet in Lake Superior; the light intensities and temperatures at these depths were lower than those reported for streams in which production was very high.

The ash-free dry weights of the Stony Point Bay regrowth were lower at twenty and thirty-five feet than at ten feet during the entire sampling period. Since the chlorophyll concentrations were of virtually the same magnitude at all depths, the amount of chlorophyll per unit of ash-free dry weight was higher at the twenty and thirty-five foot depths than at the ten foot depth. This difference occurred on nearly every sampling day. In order to test the significance of the chlorophyll concentration as a measure of biomass accumulation, correlation coefficients were calculated for total chlorophyll and total numbers of organisms at each depth. The two parameters correlated very well, the coefficients ranging from +0.782 ($P=0.02$) at the thirty-five foot depth to +0.992 ($P=0.001$) at the twenty foot depth. The coefficient for the ten foot samples was +0.950 ($P=0.001$). Regression

TABLE XII

DRY AND ASH-FREE DRY WEIGHTS OF PERIPHYTON OCCURRING AS REGROWTH, STONY POINT BAY, LAKE SUPERIOR, 1967 MILLIGRAMS PER SQUARE CENTIMETER OF ROCK SURFACE

	Dry Weight				Ash-free Dry Weight		
	Depth in Feet				Depth in Feet		
Date	10	20	35	Date	10	20	35
7-31	0.68	0.28	0.62	7-31	0.06	0.02	0.04
8-2	0.54	0.27	0.30	8-2	0.17	0.01	0.09
8-4	1.65	0.80	0.59	8-4	0.23	0.18	0.17
8-8	1.92	1.83	0.78	8-8	0.45	0.18	0.13
8-14	5.03	6.96	5.36	8-14	0.64	0.57	0.54
8-25	13.18	7.49	12.82	8-25	1.21	0.52	0.77
8-28	16.53	11.71	6.10	8-28	0.49	0.37	0.26
9-5	7.97	9.48	4.22	9-5	1.03	0.40	0.75
9-15	26.49	10.41	12.75	9-15	0.43	0.24	0.29
11-9	-*	-*	7.02	11-9	-*	-*	0.13

*No sample collected

lines for the estimation of numbers of organisms from the regrowth chlorophyll concentrations at each depth are shown in Figures 55 through 57. Good correlation at each depth indicates that chlorophyll concentration is a good parameter of the biomass of periphyton as long as sampling is always done at the same depth.

The photosynthetic rates exhibited by the regrowth samples did not increase smoothly on a unit area basis as did the pigment concentrations and weights (see Figure 58). For the first five days of incubation, no oxygen production could be demonstrated by use of the respirometer. However, on August 8, the photosynthetic rate for the ten foot sample was 5.54 microliters of oxygen per hour per square centimeter; for the twenty foot sample, 4.65 microliters/hour/cm^2; and for the thirty-five foot sample, 3.85 microliters/hour/cm^2. Corresponding values for August 14 were 23.1, 19.5, and 21.1 microliters/hour/cm^2. After August 14, the rates decreased rather than following the general pattern of increase exhibited by the parameters of biomass. The rates at ten, twenty, and thirty-five feet on September 15 were 14.8, 12.6, and 17.6 microliters/hour/cm^2. Until August 14, the ten foot samples produced the highest photosynthetic rate; after that date, the thirty-five foot samples showed the greatest photosynthetic activity. The photosynthetic rates, on a unit area basis, did not correlate well at all with total numbers of organisms. In fact, the correlation coefficients were negative at all depths, ranging from -0.213 ($P=0.10$) for the twenty foot samples to -0.791 ($P=0.01$) for the ten foot samples.

When the photosynthetic rates were expressed as assimilation values rather than on a unit area basis, the inconsistency in photosynthetic efficiency during the regrowth period became obvious. For example, the assimilation value for the twenty foot sample on August 8 was 3.01 grams of carbon fixed per hour per gram of chlorophyll; however, by August 14 the value had risen to 8.53 grams C/hour/gram of chlorophyll. The assimilation value returned to 3.04 grams C/hour/gram of chlorophyll on August 28, and then fell further to 2.06 grams C/hour per gram of chlorophyll on September 15. All of these values are higher than those calculated for naturally occurring periphyton in Stony Point Bay in 1967, although by September 15 the figures are not significantly different. By comparing the highest total chlorophyll concentrations attained during the regrowth study (September 15) with the average concentration for the naturally occurring periphyton of Stony Point Bay, it is seen that the regrowth never approached the natural level. At ten feet, the amount of chlorophyll in the regrowth sample was only twenty-nine per cent of that present in the naturally occurring growth; corresponding figures for the twenty and thirty-five foot depths are forty-two and twenty-seven per cent. However, the photosynthetic rate of the regrowth samples, on a unit area basis, reached ninety-nine per cent of the rate exhibited by the natural population at the ten foot level. At the twenty foot depth, the figure was 101 per cent, and at thirty-five feet, seventy-two per cent. It is not surprising that the regrowth population reacted in a different manner to the test conditions than did the natural population. Waters (1961) states that developing populations cannot

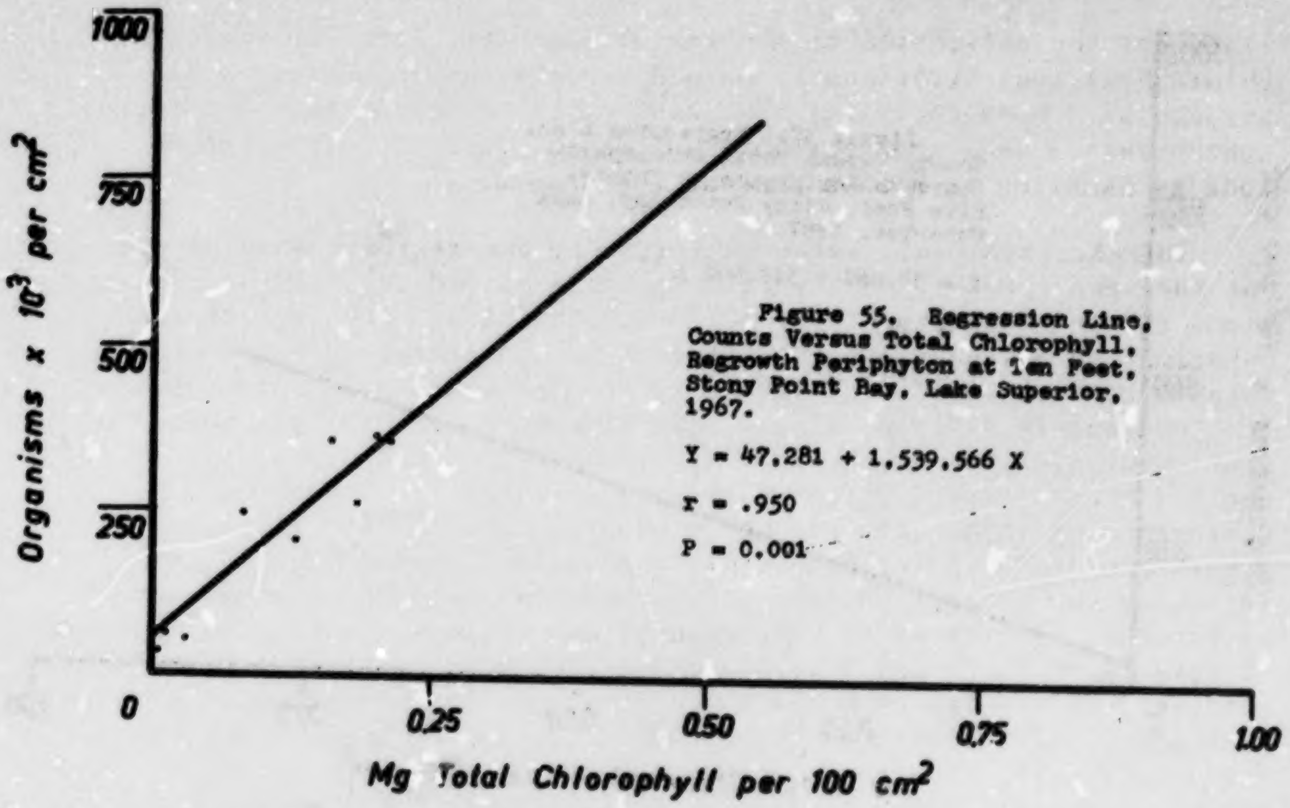

Figure 55. Regression Line, Counts Versus Total Chlorophyll, Regrowth Periphyton at Ten Feet, Stony Point Bay, Lake Superior, 1967.

Y = 47,281 + 1,539,566 X

r = .950

P = 0.001

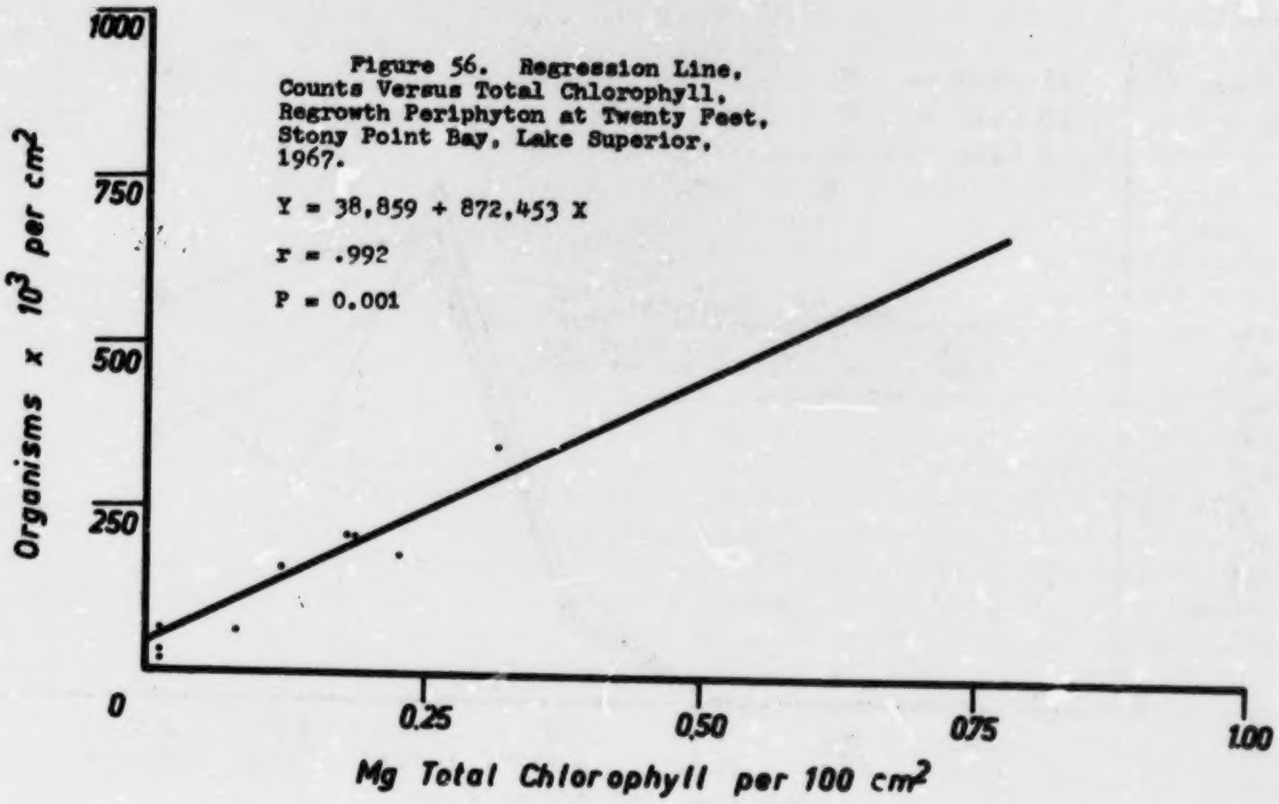

Figure 56. Regression Line, Counts Versus Total Chlorophyll, Regrowth Periphyton at Twenty Feet, Stony Point Bay, Lake Superior, 1967.

Y = 38,859 + 872,453 X

r = .992

P = 0.001

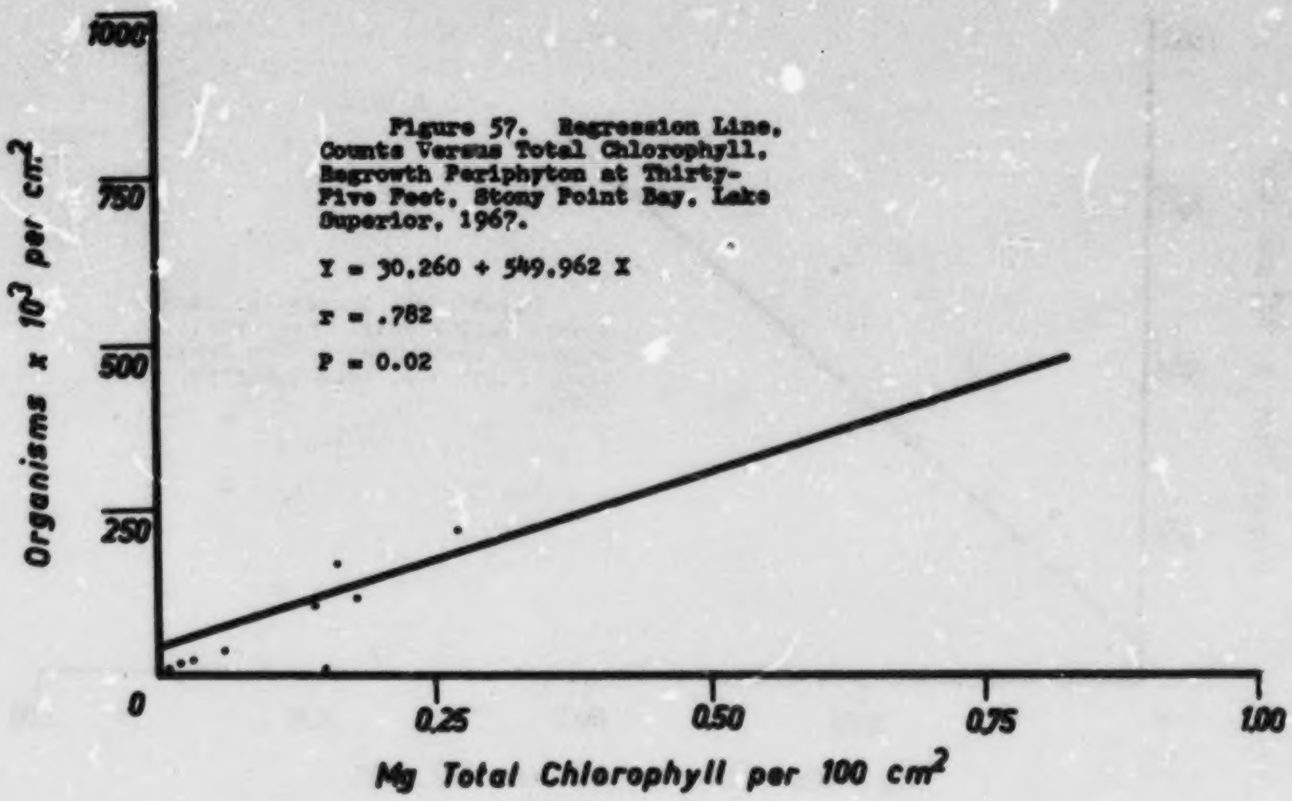

Figure 57. Regression Line, Counts Versus Total Chlorophyll, Regrowth Periphyton at Thirty-Five Feet, Stony Point Bay, Lake Superior, 1967.

$Y = 30.260 + 549.962\ X$

$r = .782$

$P = 0.02$

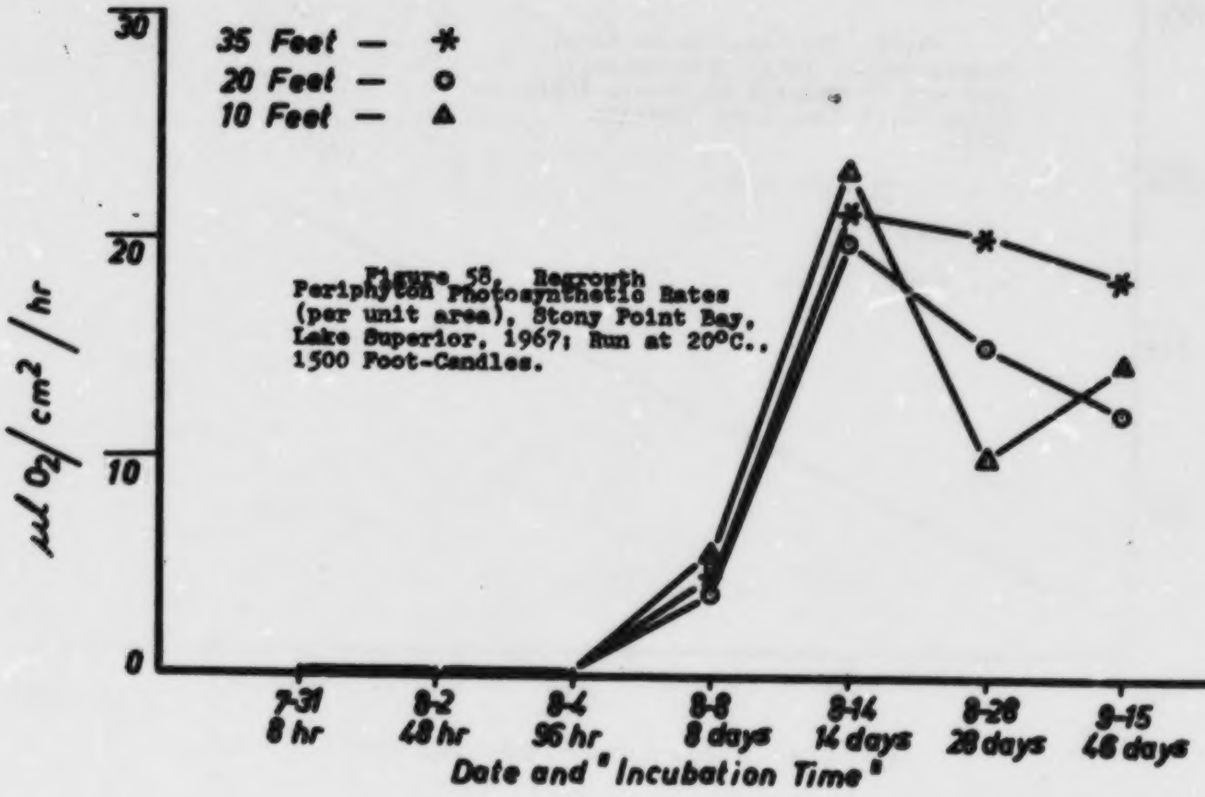

Figure 58. Regrowth Periphyton Photosynthetic Rates (per unit area), Stony Point Bay, Lake Superior, 1967; Run at 20°C., 1500 Foot-Candles.

be expected to reflect the same relationship to external factors as those which have long since reached a maximum level of biomass. That contention is strongly supported by the apparent discrepancy between the photosynthetic rates of natural and regrowth periphyton communities under the standard test conditions.

Naturally Occurring Periphyton, North Shore Stations

The eleven north shore stations sampled during the summer of 1967 are presented in Table XIII. The position of each of these sampling points in relation to one another along the north shore of Lake Superior is shown by Figure 59. Detailed sketch maps of each sampling area (Figures 60 through 70) are presented. Periphyton samples were taken from the standard depths at each station on two separate occasions. The organisms growing in these areas were studied primarily to determine whether there are significant local differences in the amount, type, and activity of the periphyton of Lake Superior's north shore. In other words, the study was conducted to test the hypothesis that the periphyton community of the prime sampling area, Stony Point Bay, was representative of a large segment of the western arm of the lake. The only data which are discussed in detail are those which appear to be unusual.

The results of the north shore investigation are summarized in Table XIV. For the purpose of comparing the various periphyton communities, the average amount of total pigment from all depths on the two sampling days was calculated for each station. The individual concentrations of chlorophylls a, b, and c at each sampling depth are presented in Figures 71 through 91. A complete tabulation of all pigment concentrations at each station is shown in Table XV.

While the mean dry and ash-free dry weights for each station are included in the summary table, the individual weights for each station are presented in Table XVI (dry weights) and Table XVII (ash-free dry weights). The average photosynthetic rate, on a unit area basis, at the 2.5 and twenty foot depths may also be seen in the summary table. The photosynthetic rates of individual samples are shown in Table XVIII. The water temperatures recorded while sampling the north shore stations are listed in Table XIX.

The total pigment concentrations of north shore periphyton ranged from 0.338 milligrams per 100 square centimeters of rock surface at Sugar Loaf Cove to 3.590 milligrams per 100 square centimeters at Lester River. The mean for all of the stations was 1.363 milligrams of pigment/100 cm^2. This value compares well with the average concentration of pigment in Stony Point Bay periphyton during the same summer (1.181 mg./100 cm^2). The area supporting the least extensive biomass, Sugar Loaf Cove, is the site of an extensive logging operation. The cove is often used as a storage area for floating logs; during such periods, the light intensity at the bottom of the cove is severely diminished. Low water temperature also limited the periphyton growth at Sugar Loaf Cove. Temperatures of 5.5° C. at a depth of twenty feet and 7.0° C. at the surface were recorded on August 31. The ratio of chlorophyll b/chlorophyll c in

TABLE XIII

PERIPHYTON SAMPLING LOCATIONS ALONG THE NORTH SHORE OF LAKE SUPERIOR

Location	Distance from Lester River in miles
1. Lester River	0
2. Knife River	13.8
3. Burlington Bay	22.1
4. Split Rock River Bay	39.4
5. Beaver Bay	48.0
6. No-Name Bay (near Little Marais)	53.9
7. Sugar Loaf Cove	69.9
8. Tofte	78.8
9. Lutsen	86.3
10. Good Harbor Bay	100.9
11. Grand Marais	106.9

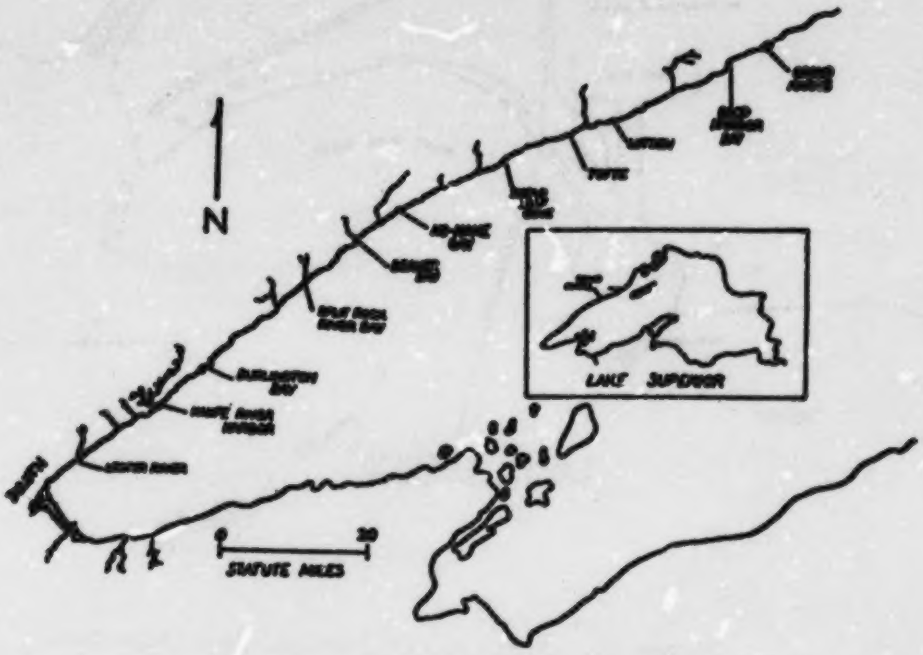
N
TOFTE
BURLINGTON BAY
LESTER RIVER
0
20
STATUTE MILES
LAKE SUPERIOR

Figure 59. Western Arm of Lake Superior Showing Relative Positions of North Shore Sampling Stations.

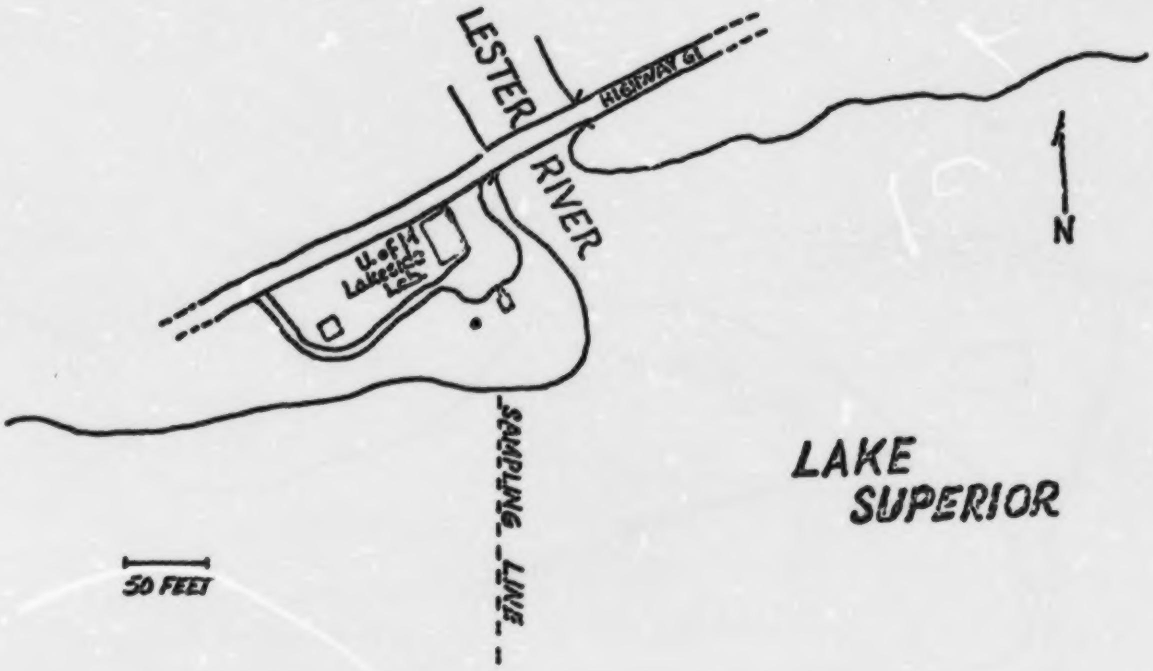
LESTER RIVER
HIGHWAY 61
U. of M Lakeside Lab
SAMPLING LINE
N
LAKE SUPERIOR
50 FEET

Figure 60. Lester River Station, Lake Superior.

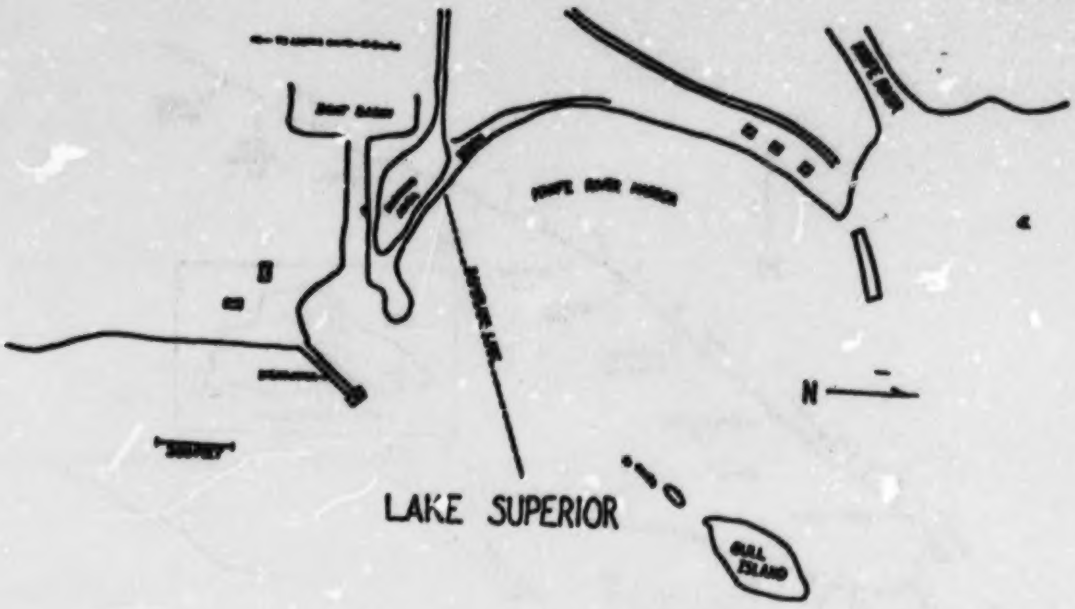
BOAT BASIN
KNIFE RIVER HARBOR
KNIFE RIVER
N
LAKE SUPERIOR
GULL ISLAND

Figure 61. Knife River Station, Lake Superior.

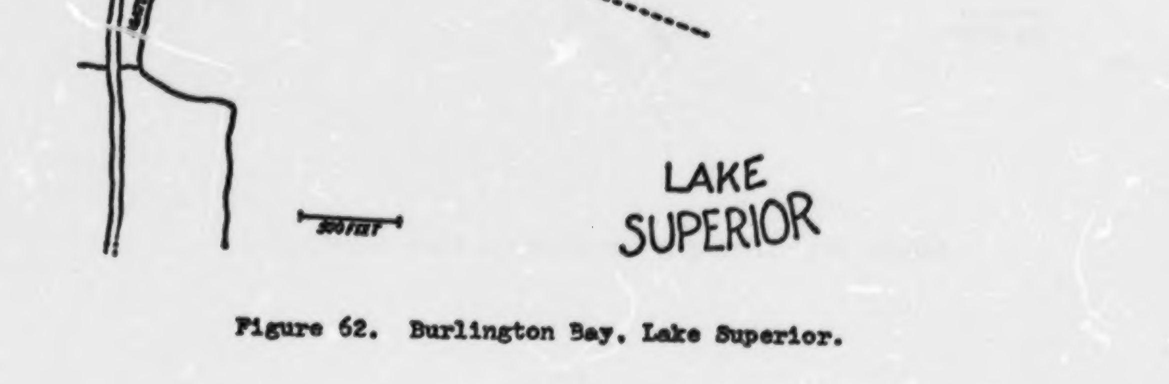
← TWO HARBORS – 1 mile
CAMPSITE
BURLINGTON BAY
N
500 FEET
LAKE
SUPERIOR

Figure 62. Burlington Bay, Lake Superior.

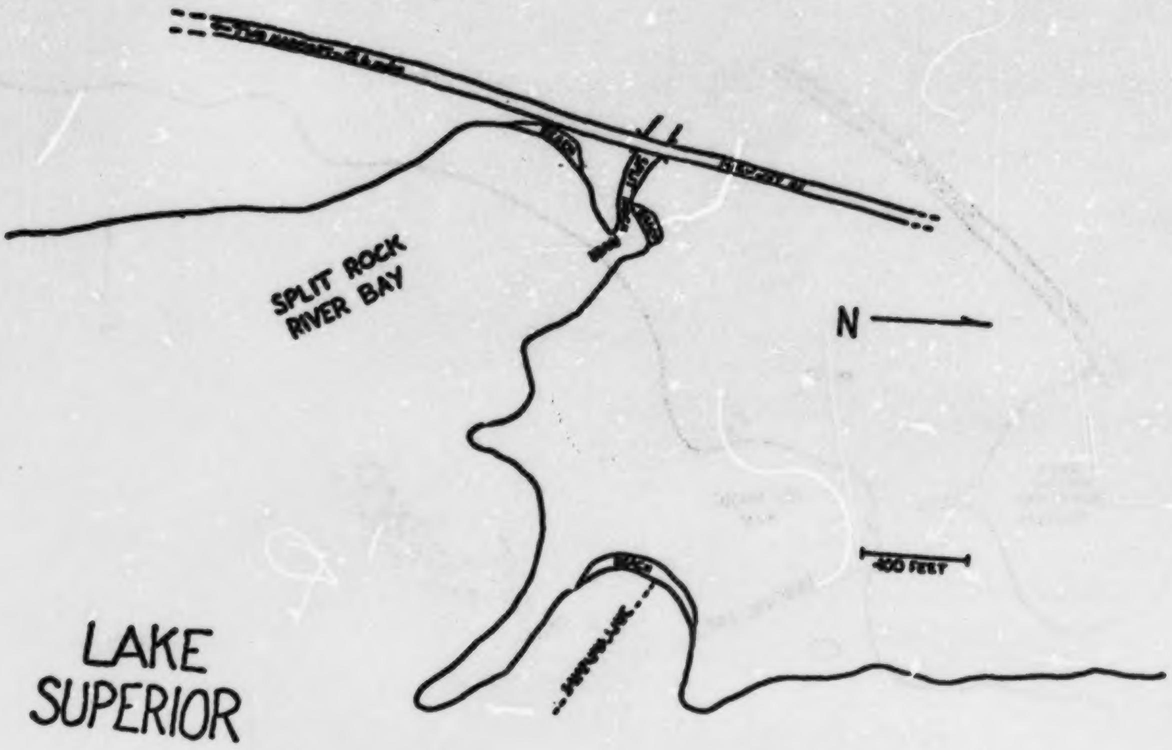
SPLIT ROCK RIVER BAY
N
BEACH
400 FEET
LAKE SUPERIOR

Figure 63. Split Rock River Bay, Lake Superior.

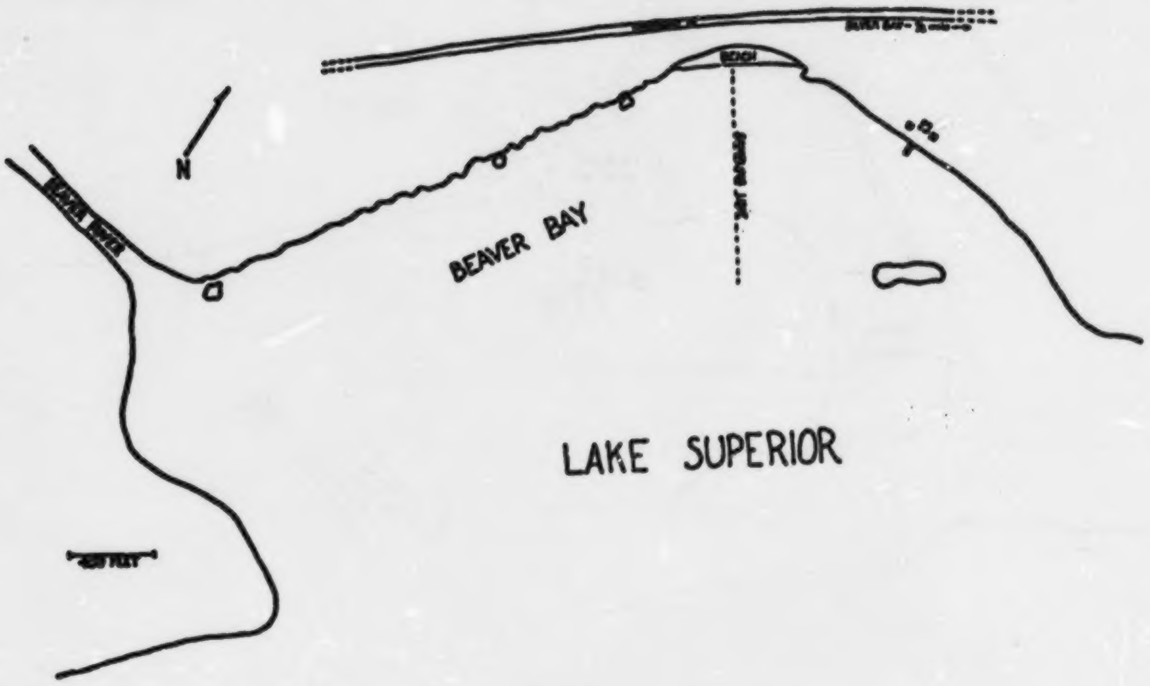
N
BEACH
BEAVER BAY
LAKE SUPERIOR
400 FEET

Figure 64. Beaver Bay, Lake Superior.

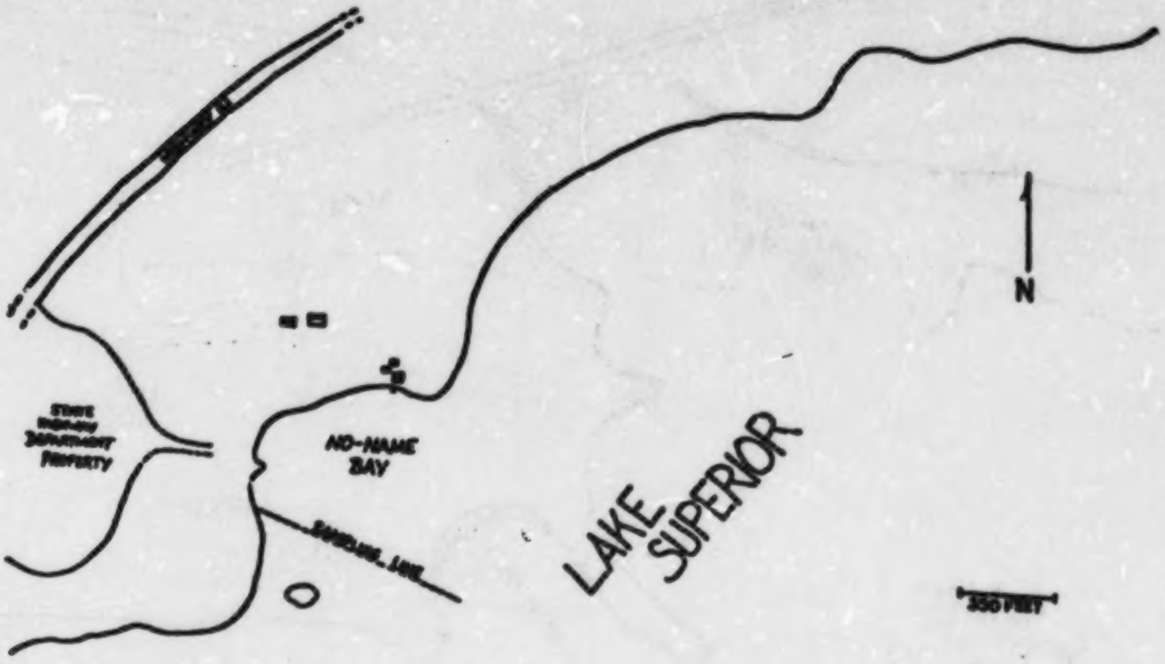
N
STATE
HIGHWAY
DEPARTMENT
PROPERTY
NO-NAME
BAY
SAMPLING LINE
LAKE
SUPERIOR
300 FEET

Figure 65. No-Name Bay, North Shore, Lake Superior.

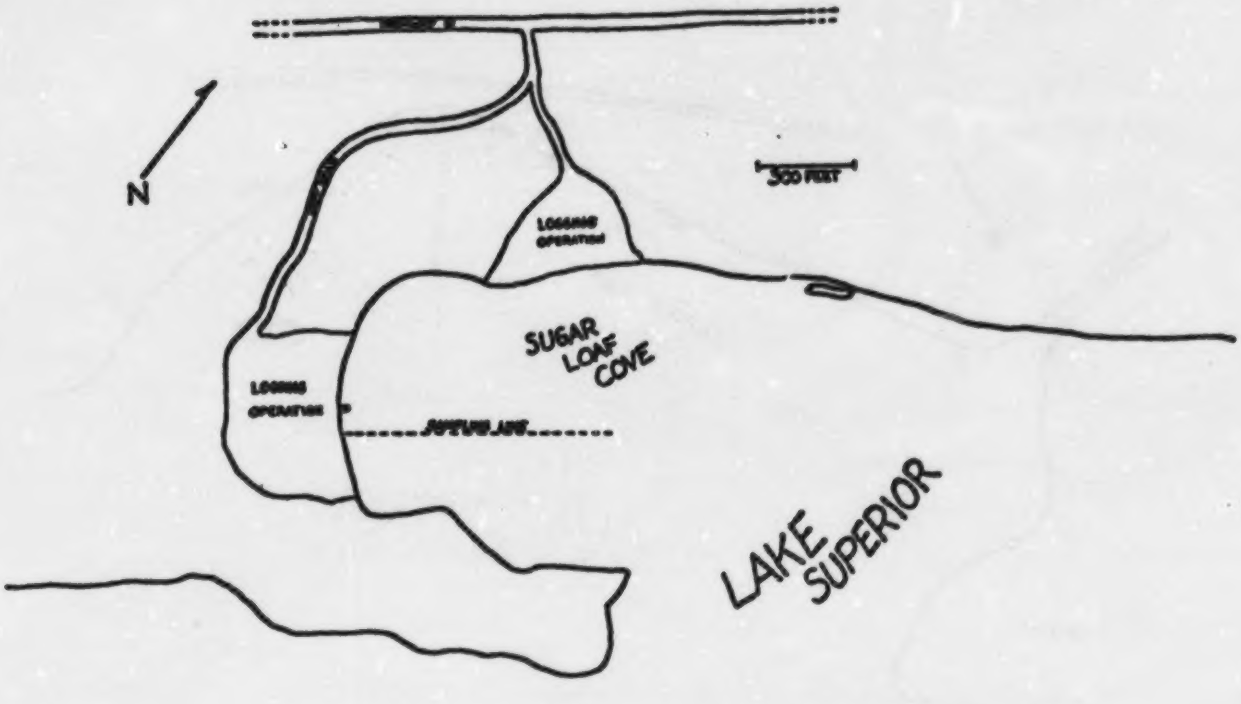
N
300 FEET
LOGGING
OPERATION
SUGAR
LOAF
COVE
LOGGING
OPERATION
SAMPLING LINE
LAKE
SUPERIOR

Figure 66. Sugar Loaf Cove, Lake Superior.

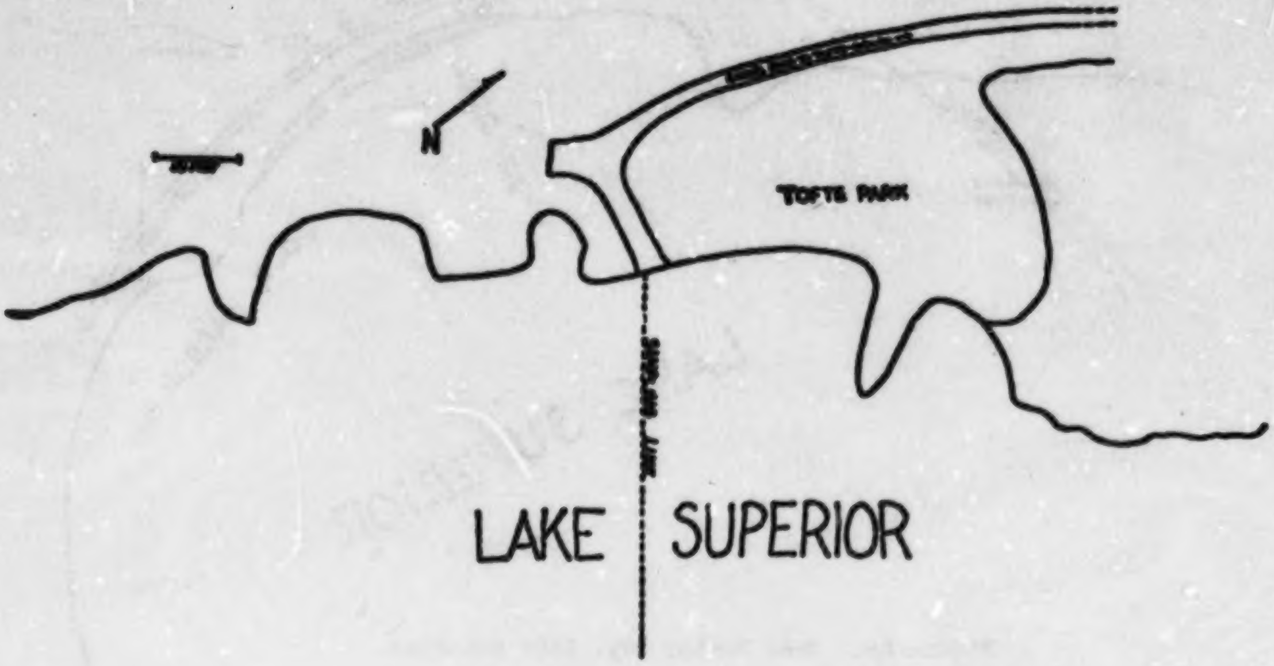
N
TOFTE PARK
SAMPLING LINE
LAKE SUPERIOR

Figure 67. Tofte Area, North Shore, Lake Superior.

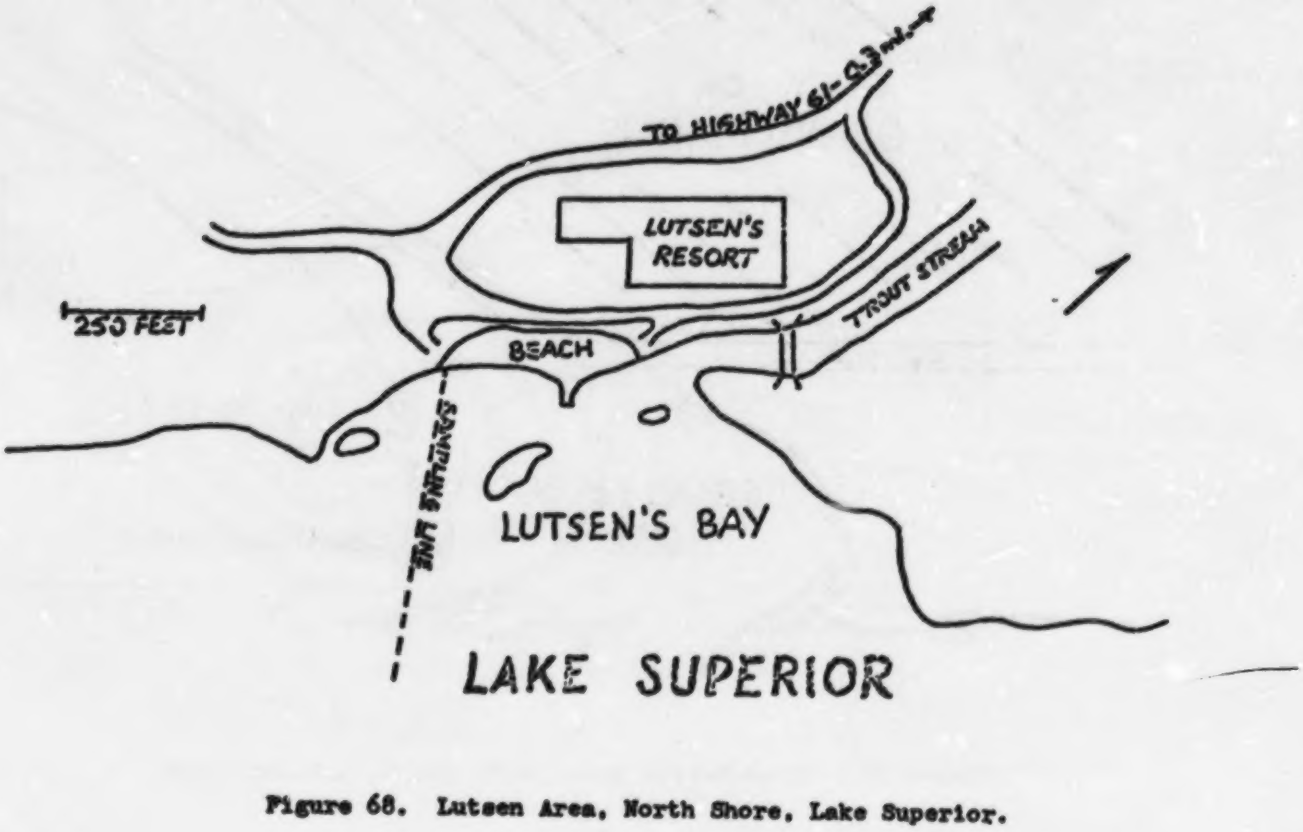
TO HIGHWAY 61 - 0.3 mi.
LUTSEN'S RESORT
TROUT STREAM
250 FEET
BEACH
SAMPLING LINE
LUTSEN'S BAY
LAKE SUPERIOR

Figure 68. Lutsen Area, North Shore, Lake Superior.

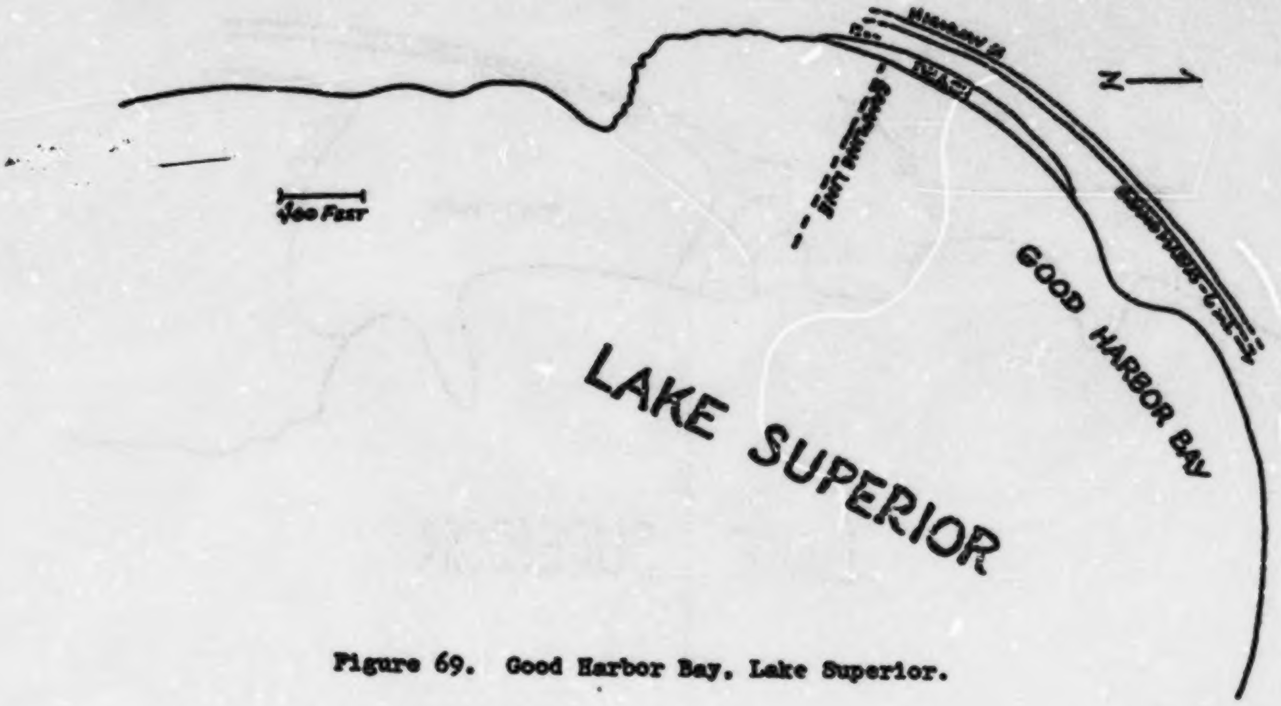
400 FEET
HIGHWAY 61
BEACH
SAMPLING LINE
N
GOOD HARBOR BAY
LAKE SUPERIOR

Figure 69. Good Harbor Bay, Lake Superior.

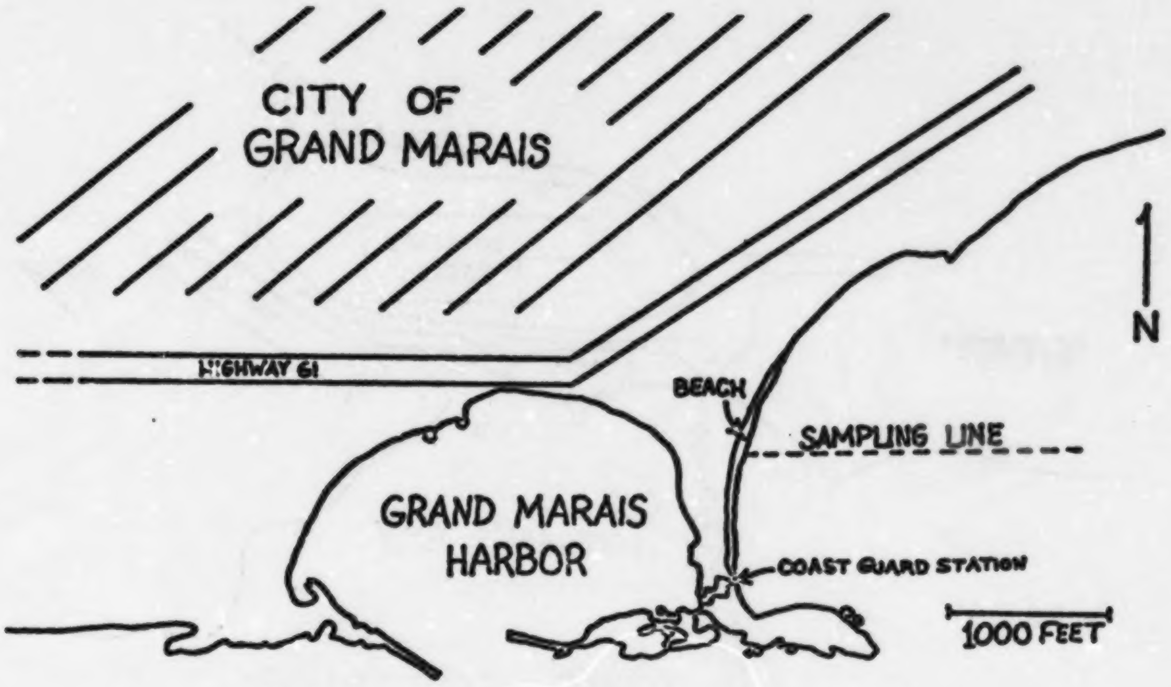
CITY OF GRAND MARAIS
HIGHWAY 61
N
BEACH
SAMPLING LINE
GRAND MARAIS HARBOR
COAST GUARD STATION
1000 FEET

Figure 70. Grand Marais Area, North Shore, Lake Superior.

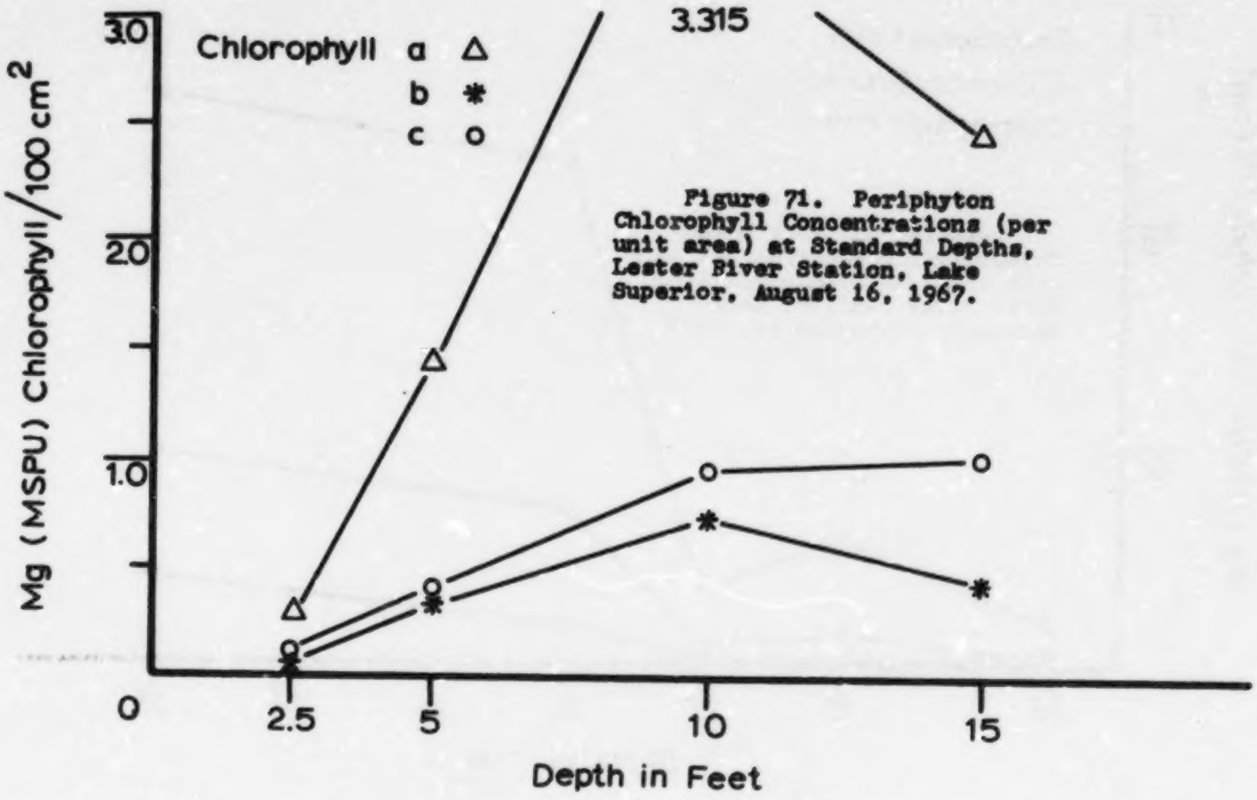

Figure 71. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Lester River Station, Lake Superior, August 16, 1967.

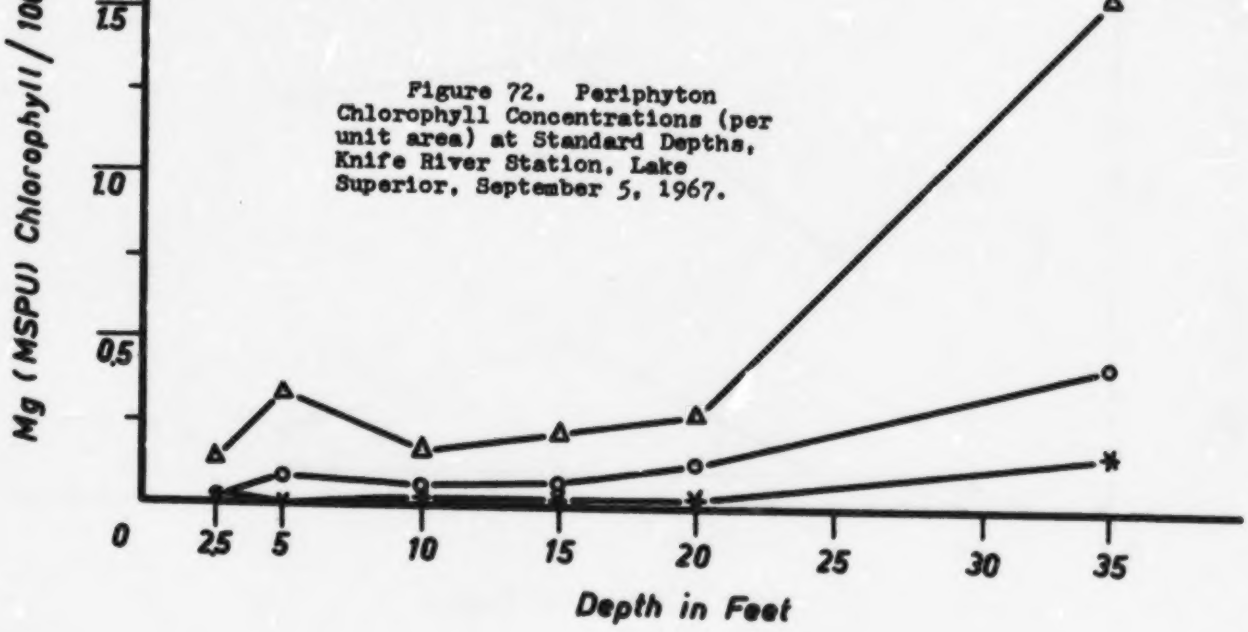

Figure 72. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Knife River Station, Lake Superior, September 5, 1967.

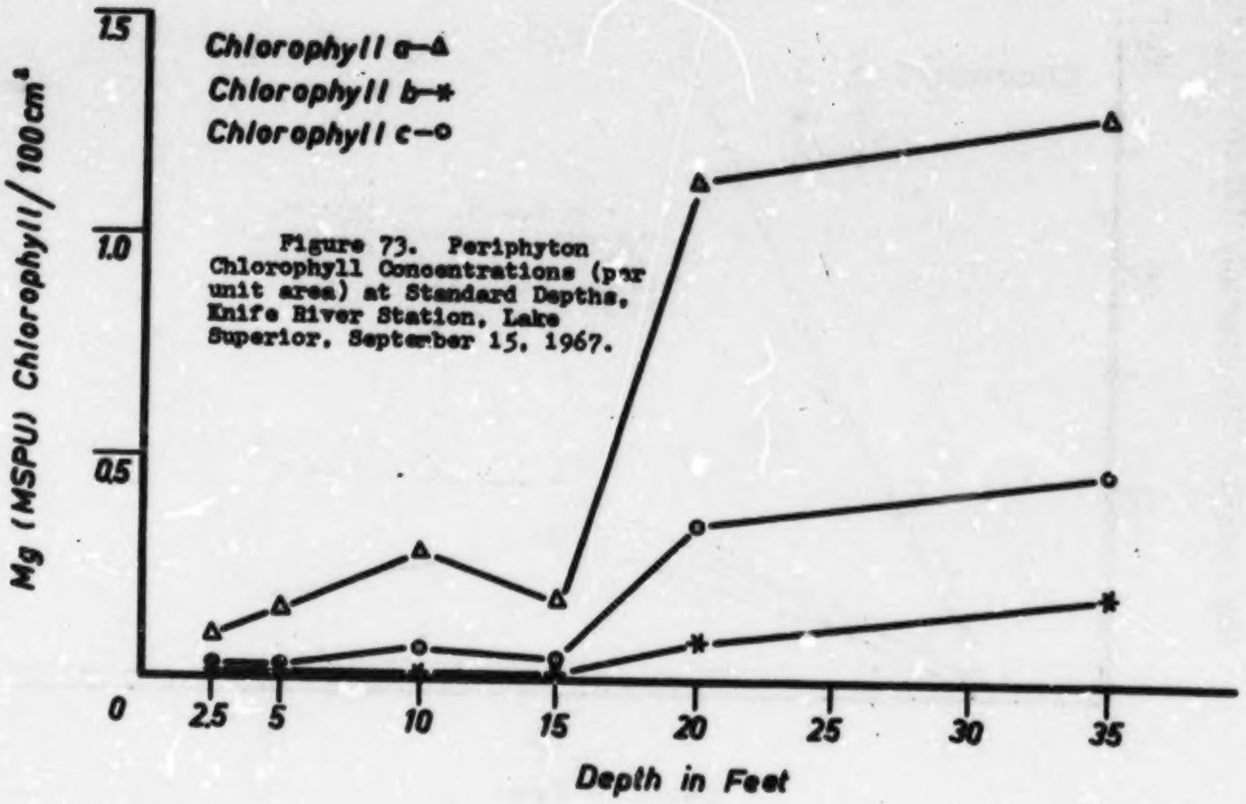

Figure 73. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Knife River Station, Lake Superior, September 15, 1967.

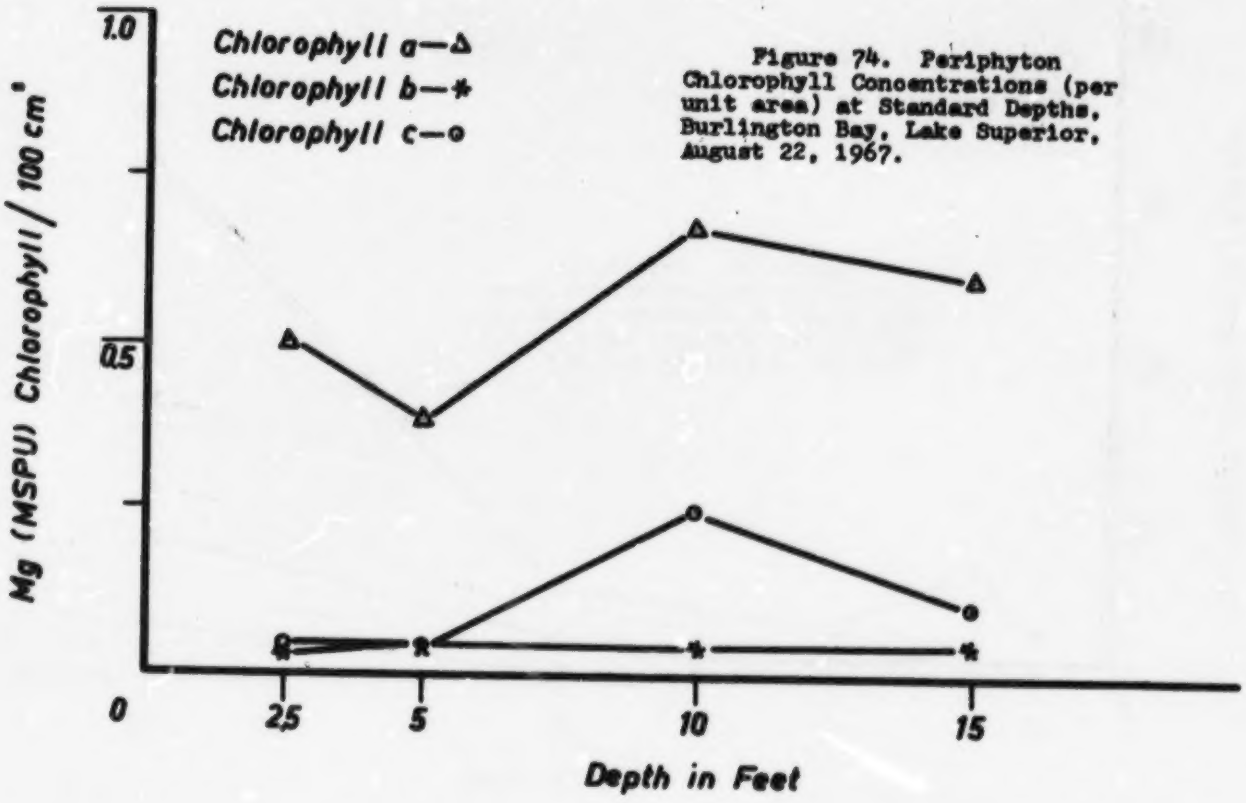

Figure 74. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Burlington Bay, Lake Superior, August 22, 1967.

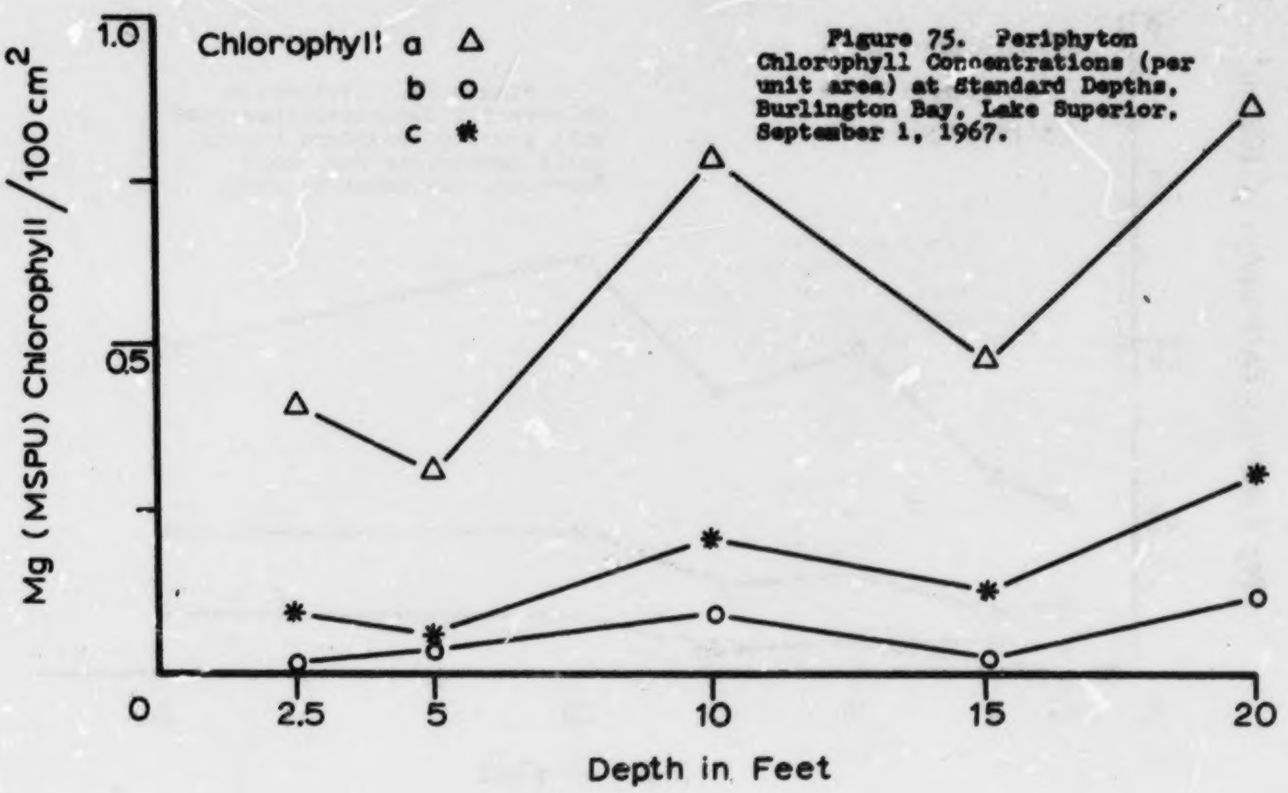

Figure 75. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Burlington Bay, Lake Superior, September 1, 1967.

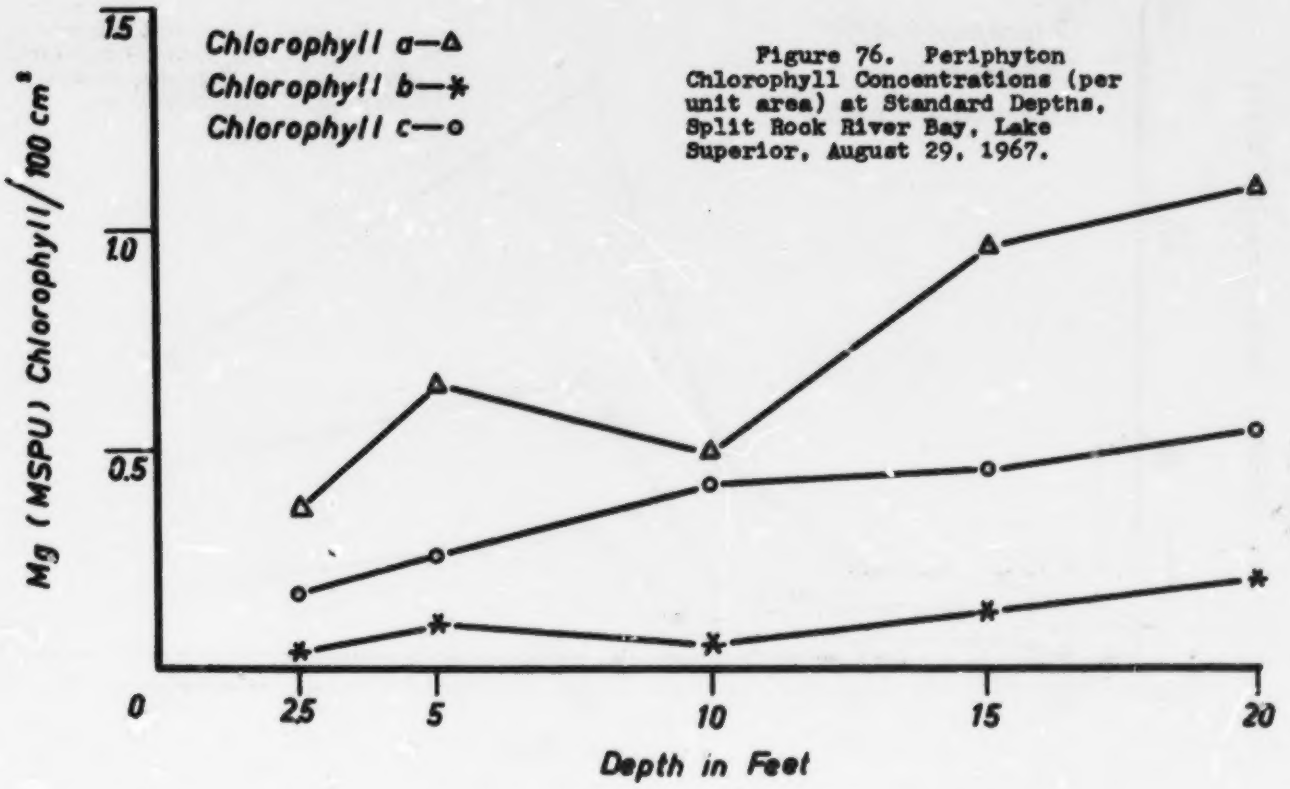

Figure 76. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Split Rock River Bay, Lake Superior, August 29, 1967.

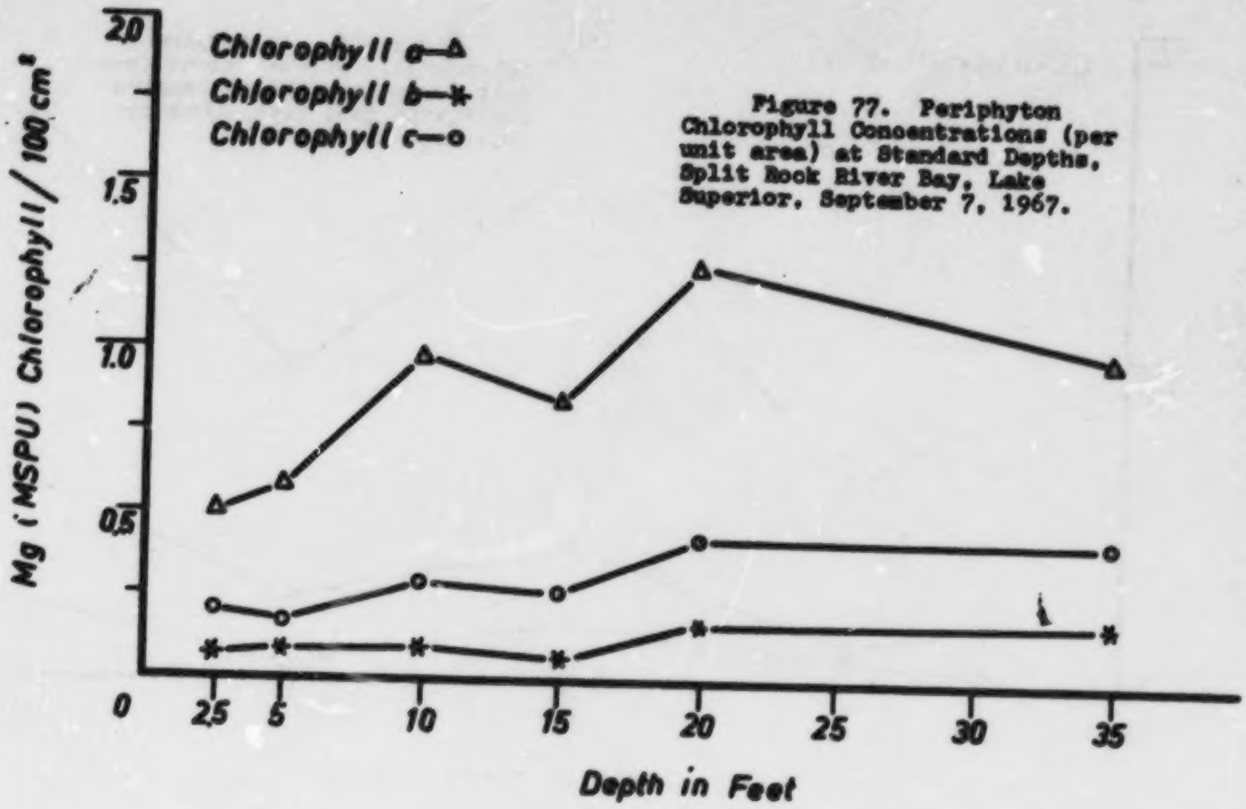

Figure 77. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Split Rock River Bay, Lake Superior, September 7, 1967.

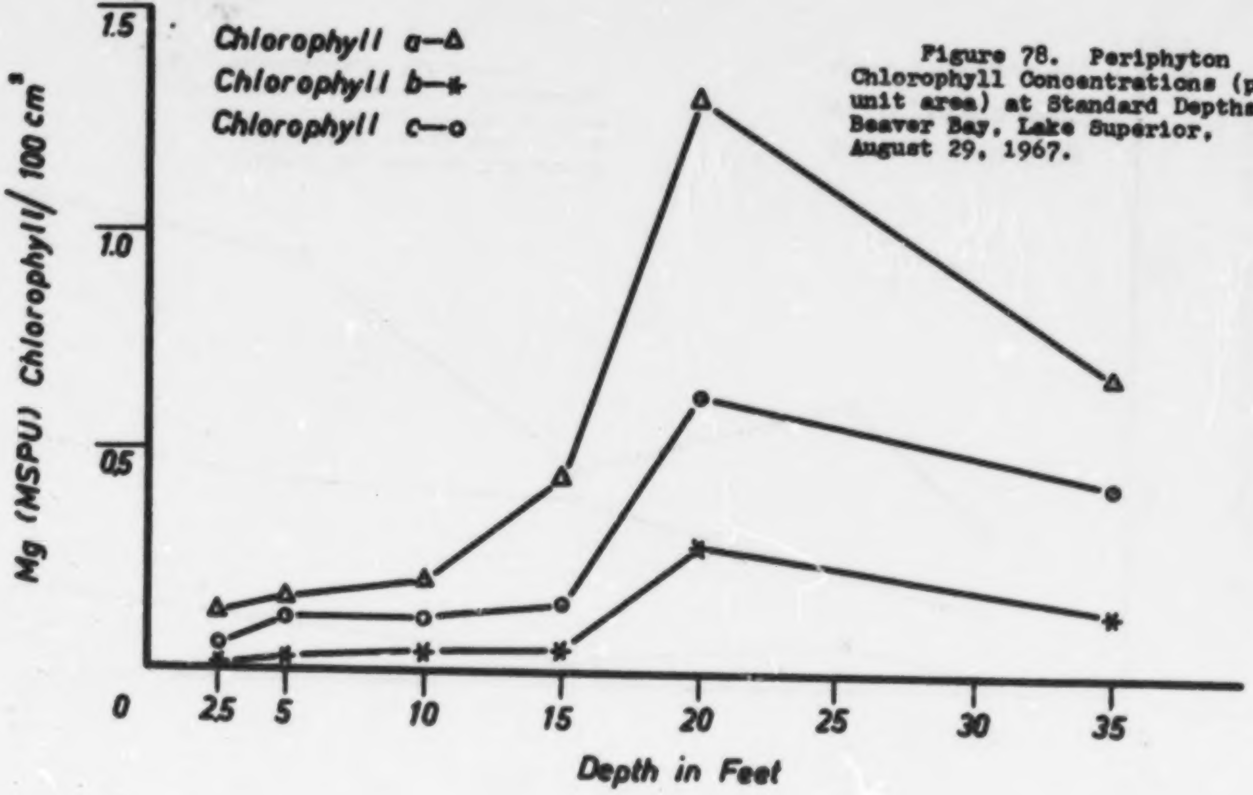

Figure 78. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Beaver Bay, Lake Superior, August 29, 1967.

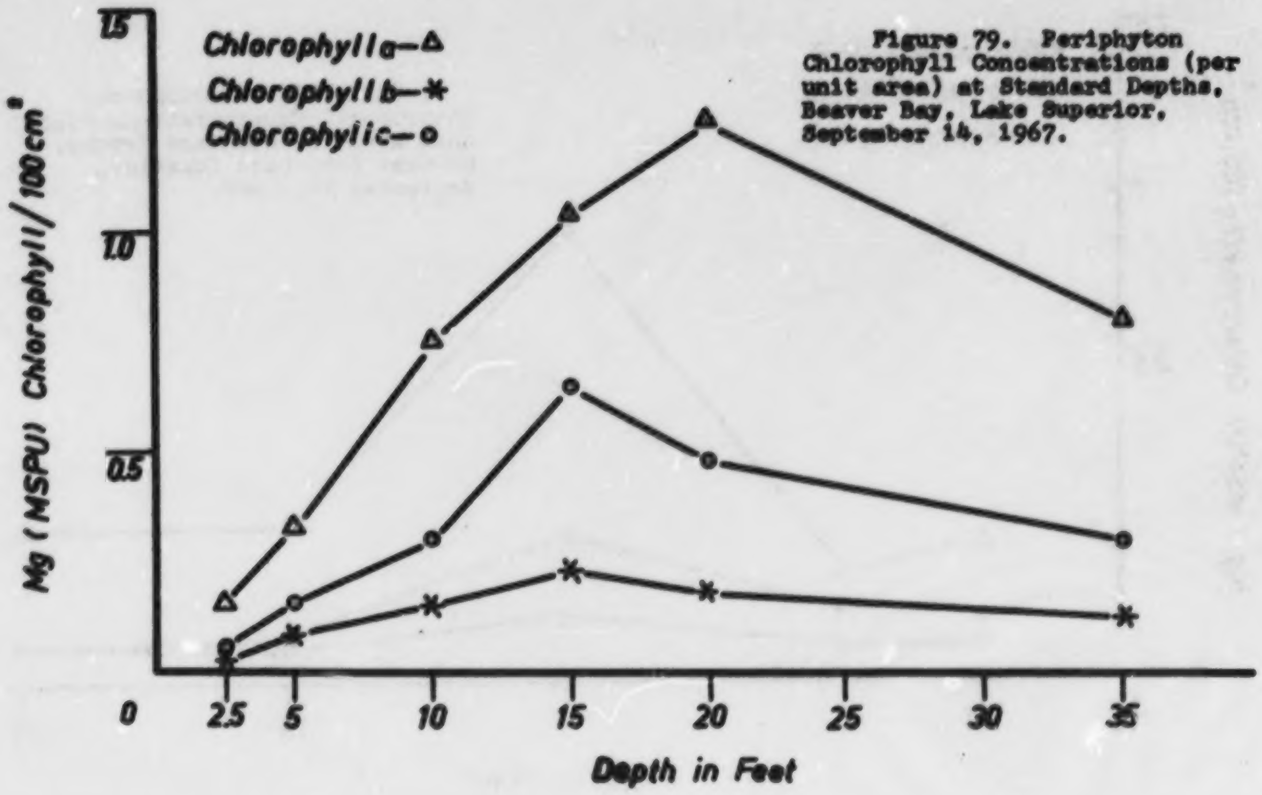

Figure 79. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Beaver Bay, Lake Superior, September 14, 1967.

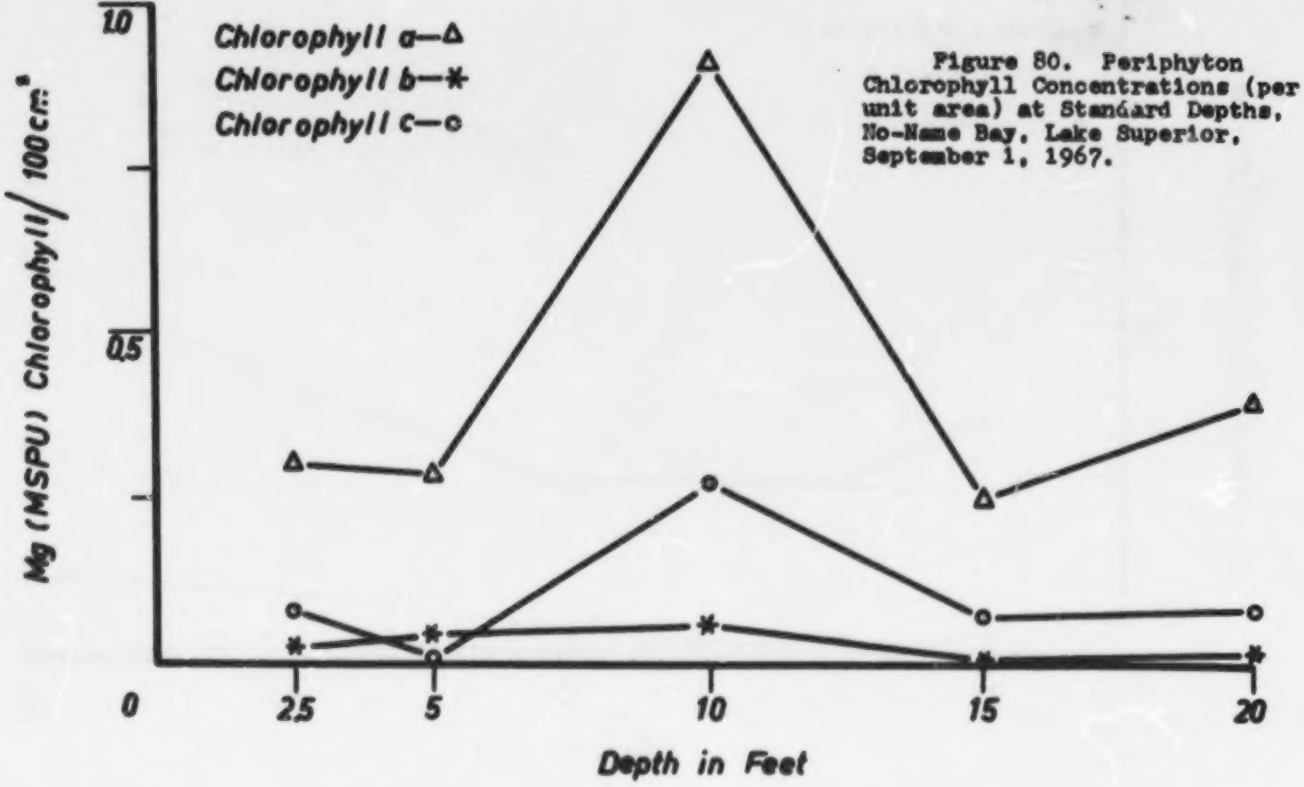

Figure 80. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, No-Name Bay, Lake Superior, September 1, 1967.

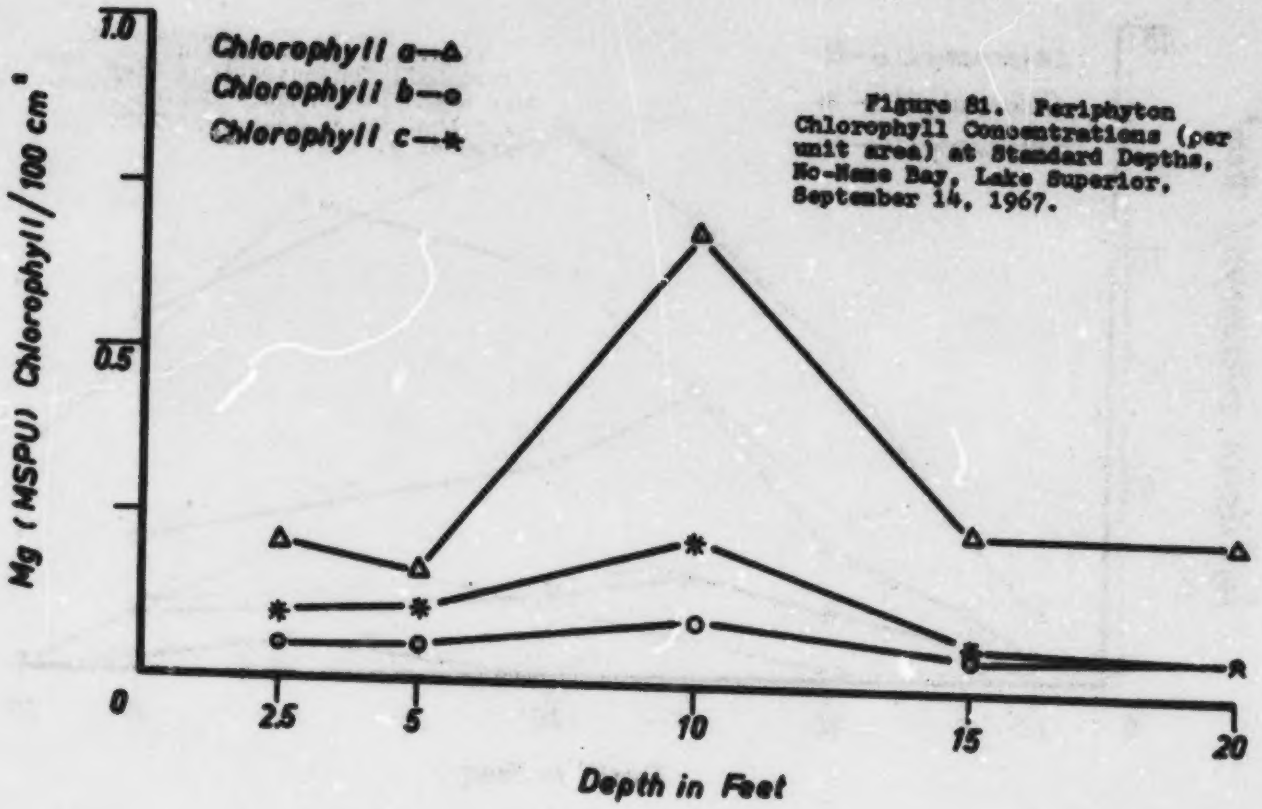

Figure 81. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, No-Name Bay, Lake Superior, September 14, 1967.

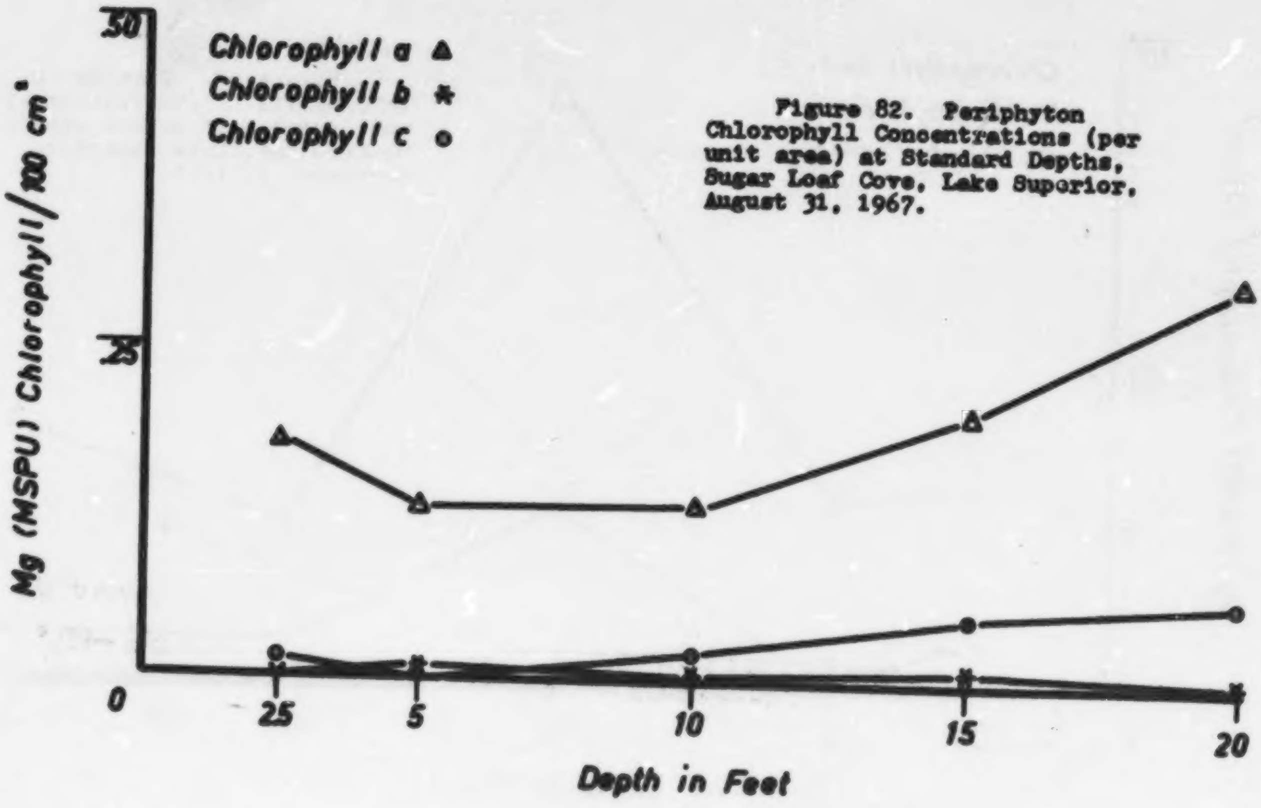

Figure 82. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Sugar Loaf Cove, Lake Superior, August 31, 1967.

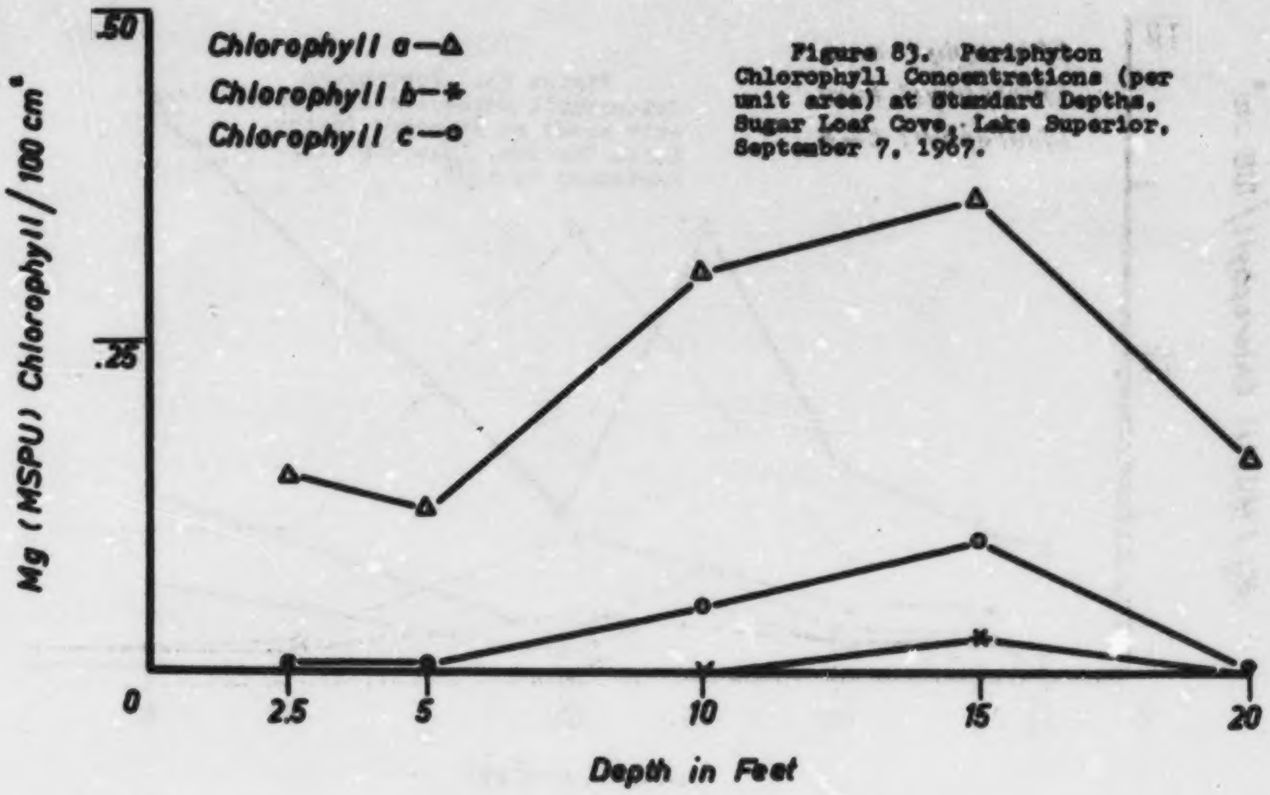

Figure 83. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Sugar Loaf Cove, Lake Superior, September 7, 1967.

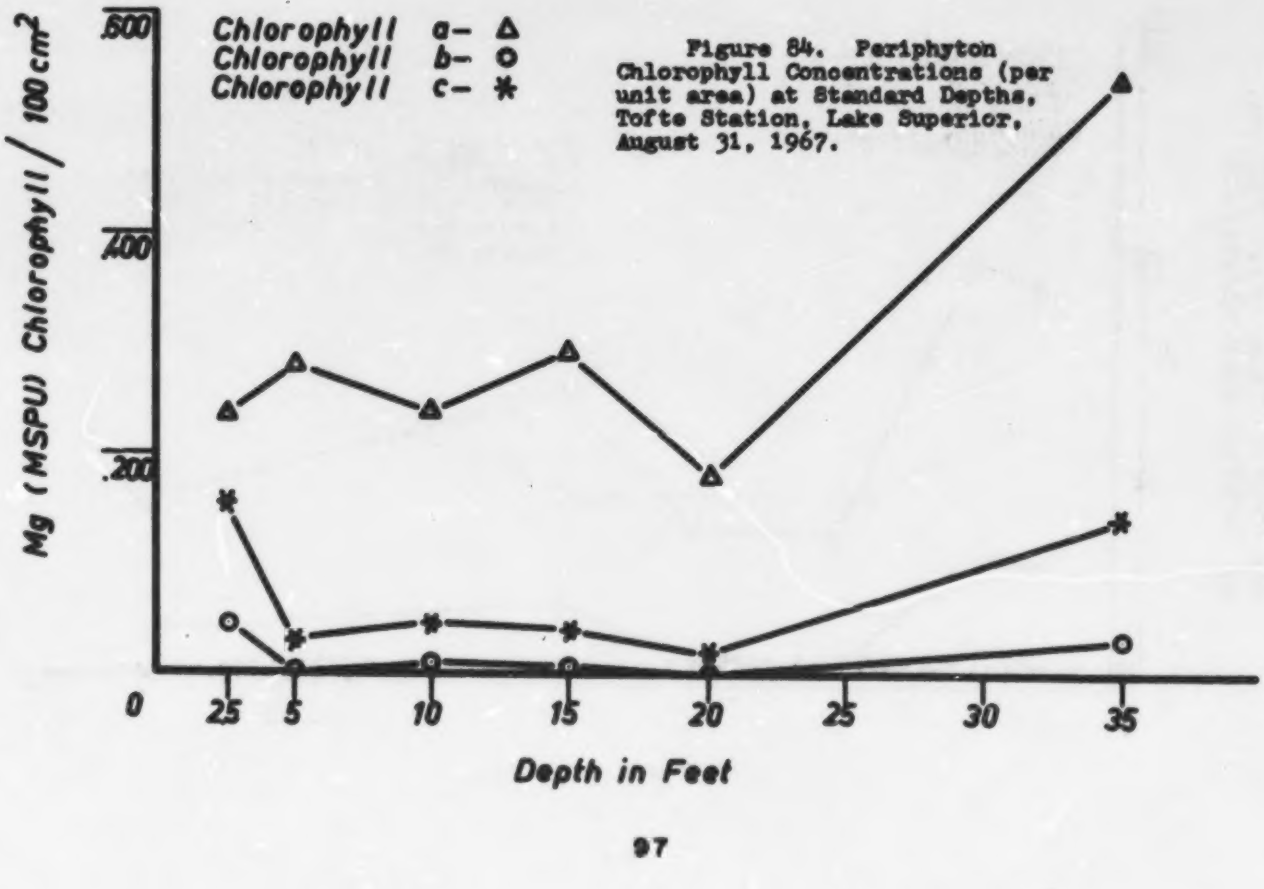

Figure 84. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Tofte Station, Lake Superior, August 31, 1967.

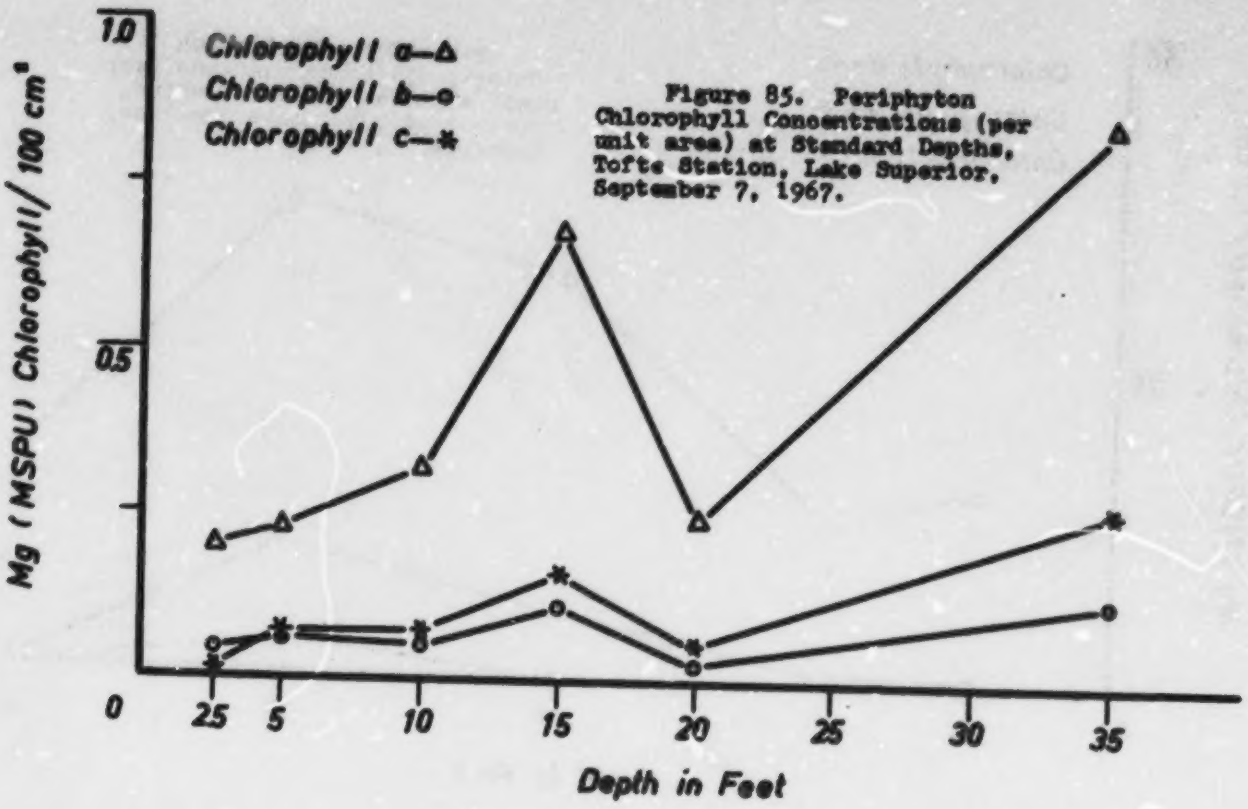

Figure 85. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Tofte Station, Lake Superior, September 7, 1967.

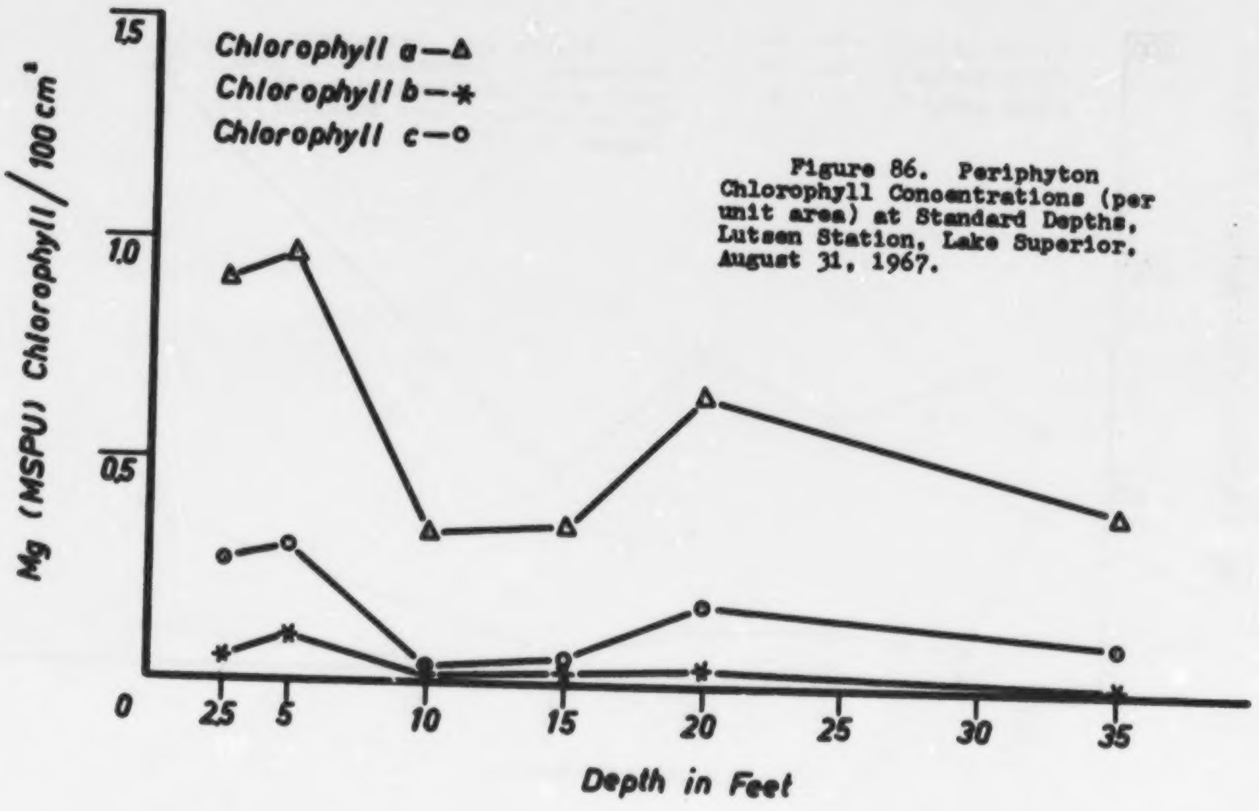

Figure 86. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Lutsen Station, Lake Superior, August 31, 1967.

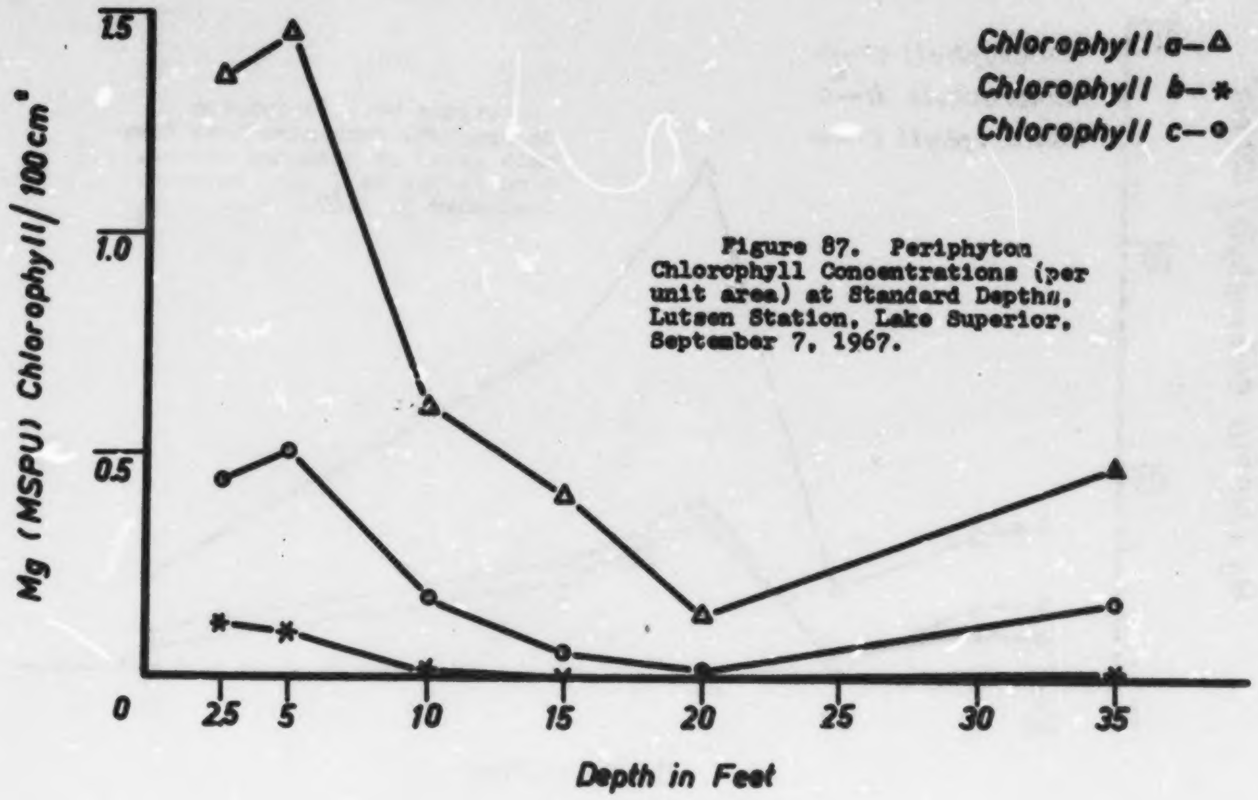

Figure 87. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Lutsen Station, Lake Superior, September 7, 1967.

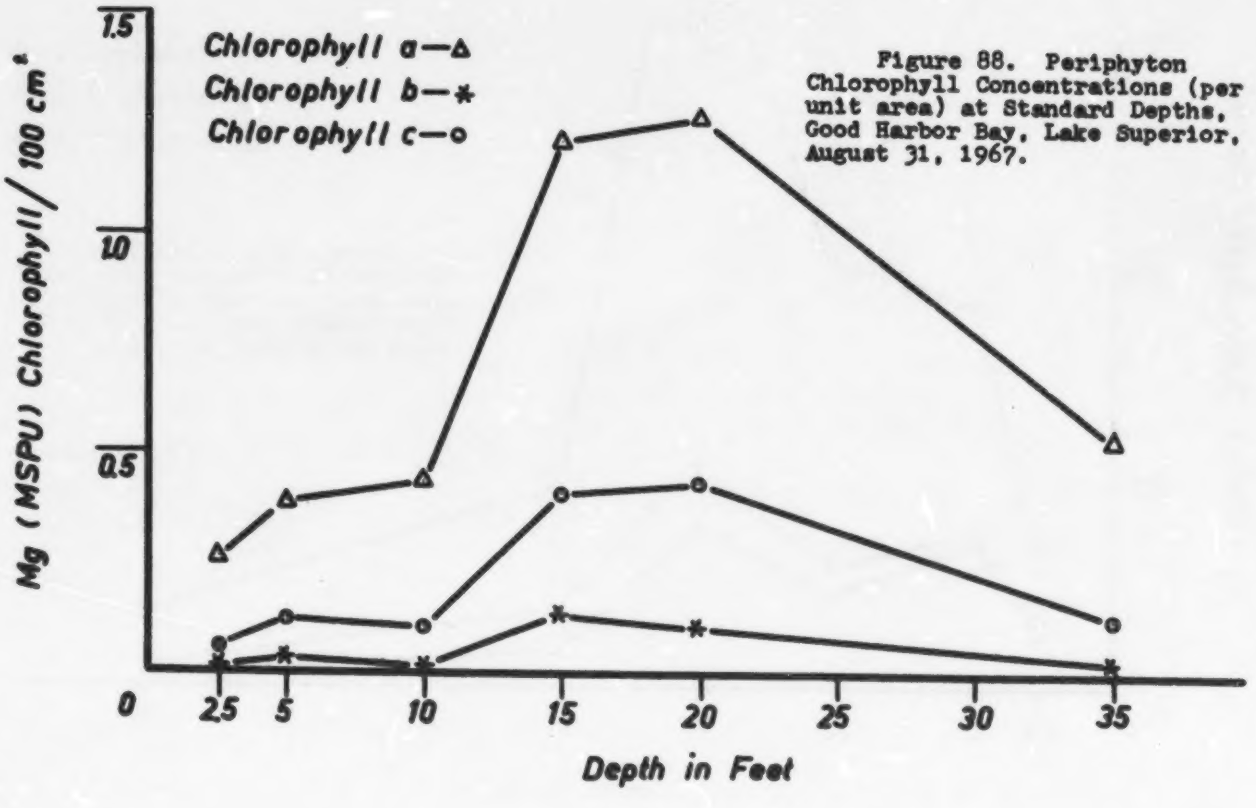

Figure 88. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Good Harbor Bay, Lake Superior, August 31, 1967.

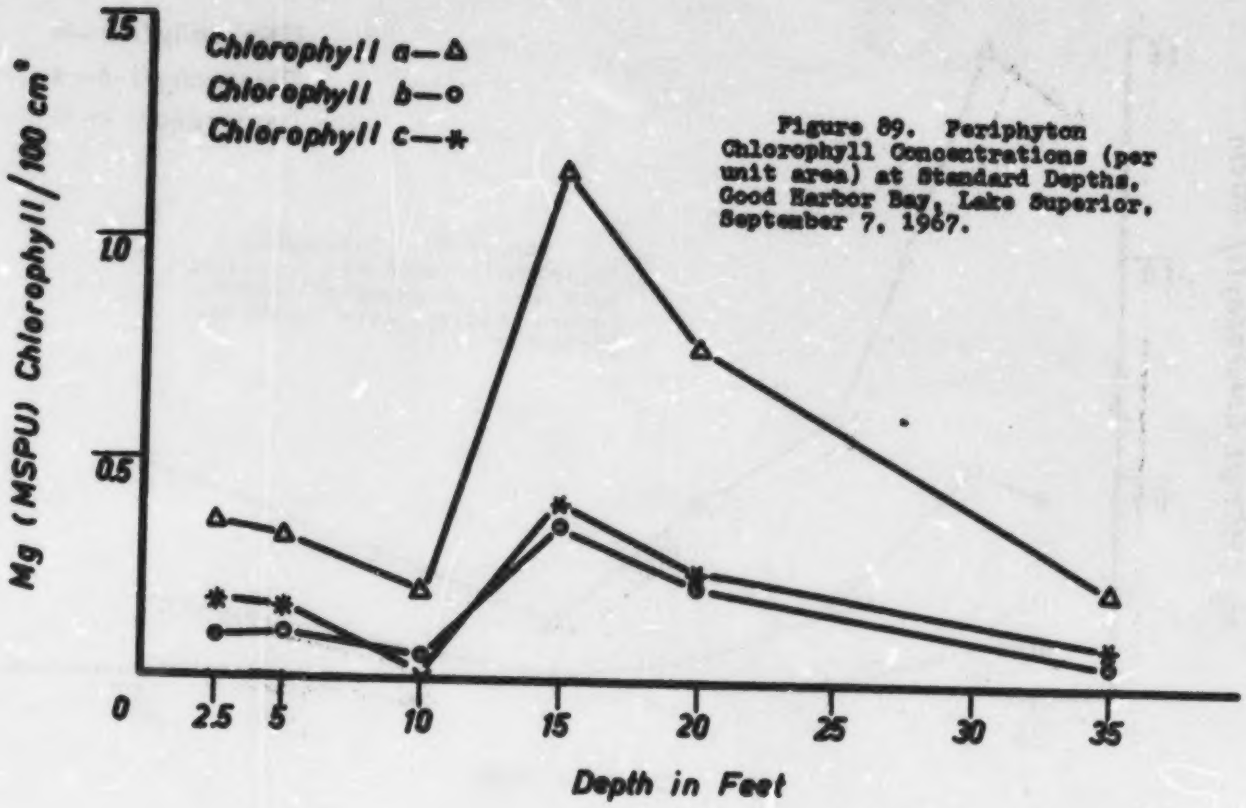

Figure 89. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Good Harbor Bay, Lake Superior, September 7, 1967.

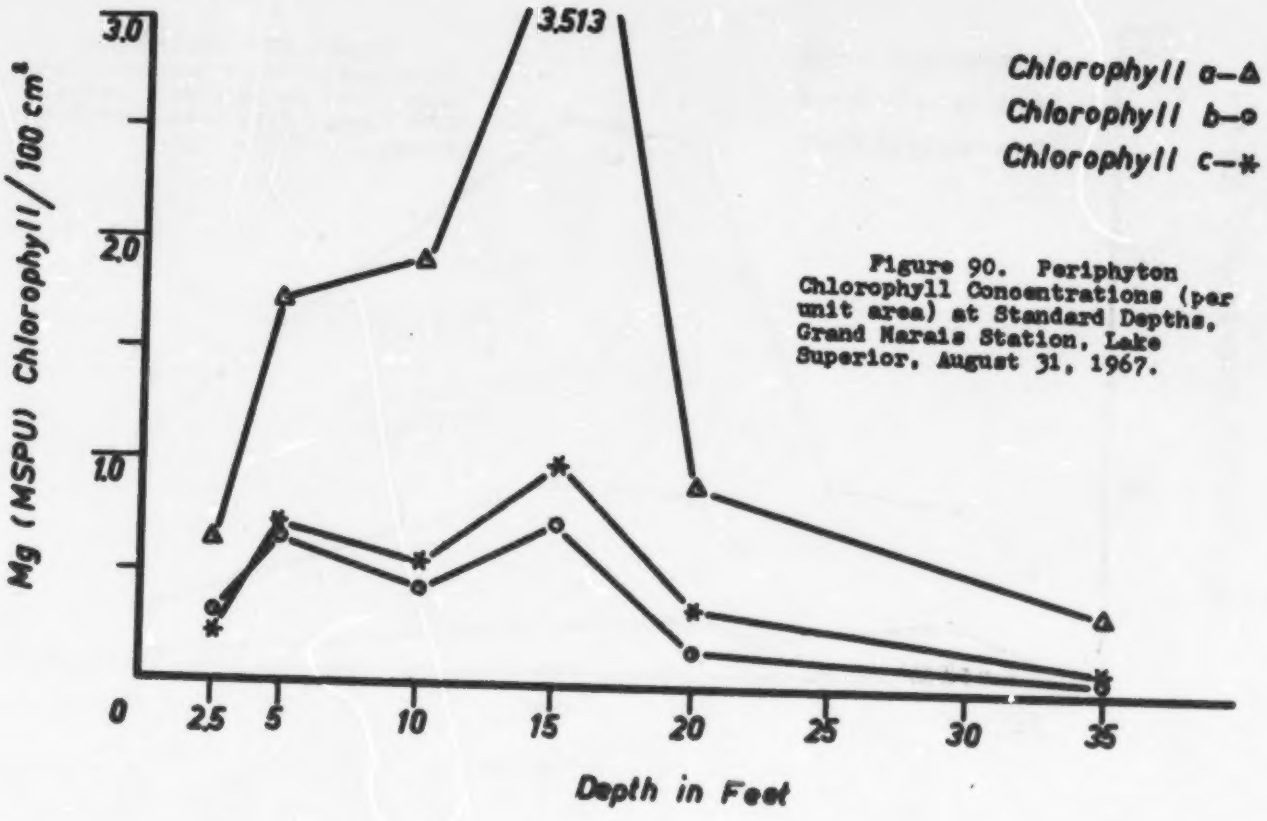

Figure 90. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Grand Marais Station, Lake Superior, August 31, 1967.

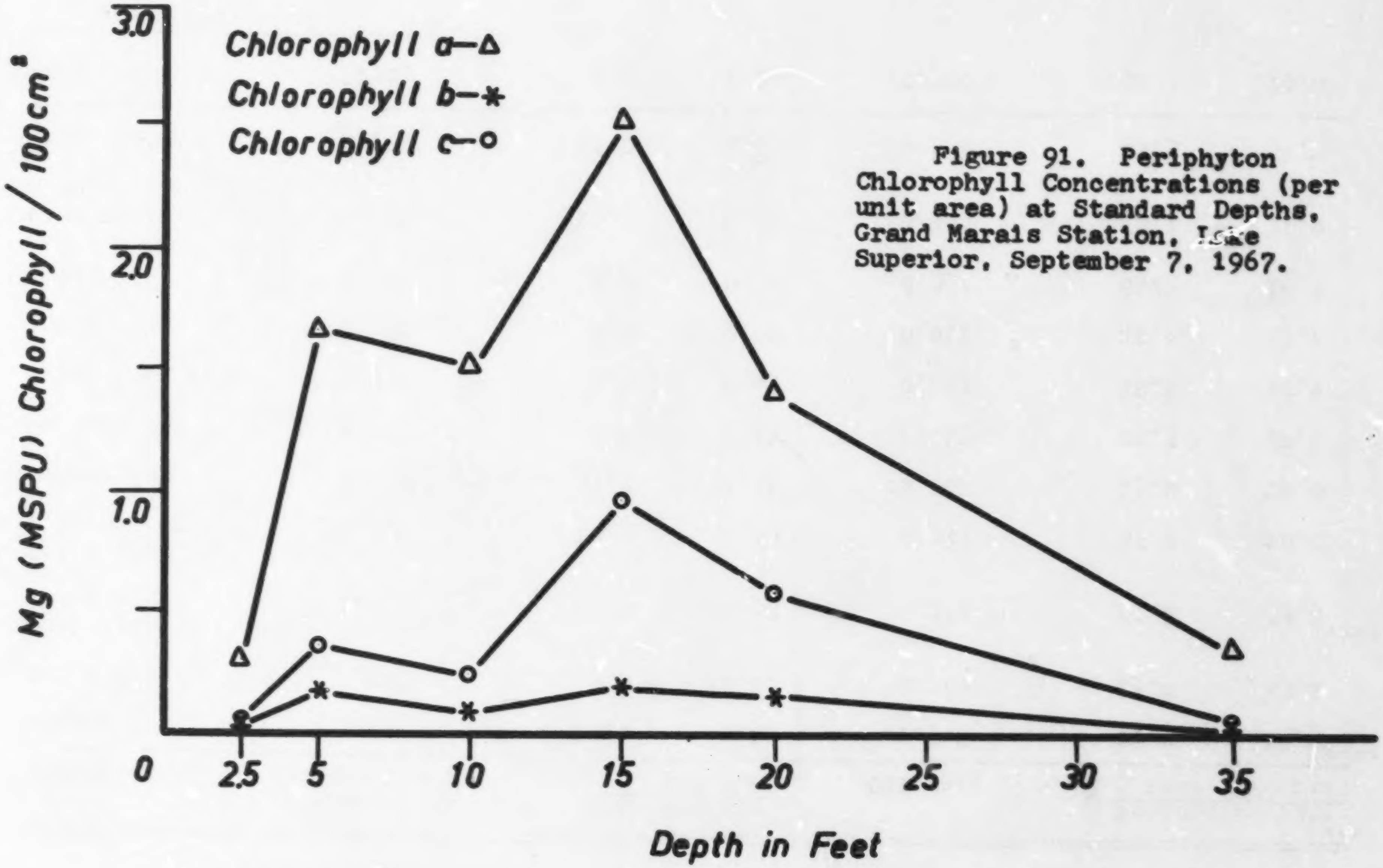

Figure 91. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Grand Marais Station, Lake Superior, September 7, 1967.

TABLE XIV

SUMMARY OF RESULTS, NORTH SHORE STATIONS, LAKE SUPERIOR, 1967

Study Area	Mean Total Pigment Conc.*	Mean Weights**		Chl. b/c	Production Rate***	
		Dry	Ash-free		2.5 feet	20 feet
Lester River	3.590	19.5	1.46	0.568	18.7	44.1****
Knife River	1.033	9.5	1.16	0.324	15.4	23.1
Burlington Bay	1.052	16.6	1.50	0.359	51.8	35.8****
Split Rock River Bay	1.256	12.5	1.35	0.347	63.9	20.2
Beaver Bay	1.264	31.5	2.31	0.402	15.2	19.0
No-Name Bay	0.767	5.6	0.84	0.413	20.3	22.2
Sugar Loaf Cove	0.338	2.7	0.61	0.143	18.8	15.2
Tofte	0.665	5.5	0.97	0.411	19.4	17.2
Lutsen	1.194	9.5	0.89	0.331	69.7	16.8
Good Harbor Bay	1.131	10.5	1.51	0.405	28.7	21.9
Grand Marais	2.700	16.0	1.60	0.588	33.3	54.5
Mean	1.363	12.7	1.29	0.390	32.3	26.4

---

*Mg+MSPU/100 cm^2

**Mg/cm^2

***Microliters O_2/hour/cm^2

****15 feet

TABLE XV

PIGMENT CONCENTRATIONS (PER UNIT AREA) NORTH SHORE STATIONS, LAKE SUPERIOR, 1967 MILLIGRAMS (MSPU) PER 100 SQUARE CENTIMETERS OF ROCK SURFACE

	Depth in Feet					
Sampling Area	2.5	5	10	15	20	35
Lester River 8-16-67						
Chlorophyll a	.283	1.431	3.315	2.455	-	-
Chlorophyll b	.066	.366	.641	.407	-	-
Chlorophyll c	.129	.455	.969	1.063	-	-
Astacin carotenoids	.000	.024	.067	.043	-	-
Non-astacin carotenoids	.138	.549	1.216	.89[illegible]	-	-
Knife River 9-5-67						
Chlorophyll a	.141	.333	.187	.220	.288	1.572
Chlorophyll b	.015	.000	.029	.013	.022	.166
Chlorophyll c	.017	.085	.034	.072	.118	.431
Astacin carotenoids	.004	.002	.013	.008	.020	.077
Non-astacin carotenoids	.085	.175	.086	.097	.107	.514
9-15-67						
Chlorophyll a	.087	.149	.282	.177	1.126	1.284
Chlorophyll b	.007	.004	.015	.006	.090	.198
Chlorophyll c	.026	.031	.063	.045	.354	.472
Astacin carotenoids	.005	.007	.006	.007	.050	.047
Non-astacin carotenoids	.034	.067	.128	.072	.380	.423
Burlington Bay 8-22-67						
Chlorophyll a	.509	.381	.676	.605	-	-
Chlorophyll b	.036	.044	.043	.047	-	-
Chlorophyll c	.040	.044	.253	.107	-	-
Astacin carotenoids	.010	.010	.029	.035	-	-
Non-astacin carotenoids	.298	.195	.324	.252		
9-1-67						
Chlorophyll a	.399	.300	.774	.476	.856	-
Chlorophyll b	.010	.037	.080	.014	.142	-
Chlorophyll c	.100	.050	.192	.164	.299	-
Astacin carotenoids	.020	.000	.017	.017	.047	-
Non-astacin carotenoids	.294	.193	.429	.234	.391	-
Split Rock River Bay 8-29-67						
Chlorophyll a	.356	.636	.481	.948	1.084	-
Chlorophyll b	.039	.101	.055	.128	.204	-
Chlorophyll c	.163	.259	.412	.456	.537	-
Astacin carotenoids	.005	.024	.031	.044	.081	-
Non-astacin carotenoids	.214	.340	.215	.307	.373	-
9-7-67						
Chlorophyll a	.494	.571	.975	.834	1.222	.972
Chlorophyll b	.072	.114	.093	.084	.182	.175
Chlorophyll c	.207	.170	.287	.263	.421	.414
Astacin carotenoids	.009	.003	.015	.032	.039	.057
Non-astacin carotenoids	.300	.363	.530	.393	.538	.356
Beaver Bay 8-29-67						
Chlorophyll a	.122	.157	.197	.444	1.303	.872
Chlorophyll b	.014	.030	.038	.055	.285	.137
Chlorophyll c	.055	.121	.119	.158	.627	.425
Astacin carotenoids	.011	.019	.021	.026	.092	.076
Non-astacin carotenoids	.052	.068	.083	.176	.456	.334
9-14-67						
Chlorophyll a	.141	.316	.759	1.034	1.249	.793
Chlorophyll b	.033	.081	.149	.232	.196	.132
Chlorophyll c	.040	.159	.306	.644	.487	.303
Astacin carotenoids	.023	.038	.047	.099	.058	.065
Non-astacin carotenoids	.070	.143	.326	.382	.535	.318
No-Name Bay 9-1-67						
Chlorophyll a	.306	.282	.916	.250	.396	-
Chlorophyll b	.029	.042	.063	.018	.023	-
Chlorophyll c	.087	.010	.273	.074	.117	-
Astacin carotenoids	.017	.002	.000	.005	.012	-
Non-astacin carotenoids	.141	.149	.499	.126	.161	-
9-14-67						
Chlorophyll a	.208	.180	.688	.231	.223	-
Chlorophyll b	.052	.055	.136	.052	.053	-
Chlorophyll c	.110	.120	.225	.060	.052	-
Astacin carotenoids	.000	.000	.008	.008	.011	-
Non-astacin carotenoids	.138	.118	.415	.140	.118	-
Sugar Loaf Cove 8-31-67						
Chlorophyll a	.176	.133	.138	.205	.302	-
Chlorophyll b	.000	.005	.004	.011	.001	-
Chlorophyll c	.012	.000	.019	.051	.084	-
Astacin carotenoids	.000	.001	.007	.013	.015	-
Non-astacin carotenoids	.094	.073	.065	.078	.125	-

continued

TABLE XV (continued)

Sampling Area	Depth in Feet 2.5	5	10	15	20	35
9-7-67						
Chlorophyll a	.146	.119	.310	.361	.167	-
Chlorophyll b	.000	.000	.000	.0028	.000	-
Chlorophyll c	.003	.015	.051	.104	.004	-
Astacin carotenoids	.011	.005	.011	.030	.006	-
Non-astacin carotenoids	.070	.061	.142	.144	.082	-
Tofte 8-31-67						
Chlorophyll a	.234	.283	.237	.289	.180	.519
Chlorophyll b	.046	.000	.011	.009	.000	.033
Chlorophyll c	.154	.029	.045	.038	.019	.142
Astacin carotenoids	.014	.010	.000	.004	.002	.015
Non-astacin carotenoids	.130	.183	.134	.136	.088	.195
9-7-67						
Chlorophyll a	.194	.233	.361	.676	.242	.841
Chlorophyll b	.045	.060	.049	.037	.024	.131
Chlorophyll c	.019	.069	.072	.169	.066	.262
Astacin carotenoids	.000	.010	.000	.009	.009	.034
Non-astacin carotenoids	.147	.190	.217	.381	.127	.319
Lutsen 8-31-67						
Chlorophyll a	.896	1.085	.339	.344	.648	.407
Chlorophyll b	.053	.093	.017	.027	.035	.012
Chlorophyll c	.267	.300	.023	.049	.186	.105
Astacin carotenoids	.004	.016	.005	.013	.013	.010
Non-astacin carotenoids	.349	.454	.155	.137	.234	.149
9-7-67						
Chlorophyll a	1.357	1.463	.600	.408	.144	.488
Chlorophyll b	.117	.094	.006	.000	.000	.010
Chlorophyll c	.436	.510	.167	.043	.004	.164
Astacin carotenoids	.016	.015	.023	.016	.004	.013
Non-astacin carotenoids	.574	.675	.275	.176	.065	.185
Good Harbor Bay 8-31-67						
Chlorophyll a	.266	.384	.423	1.190	1.267	.524
Chlorophyll b	.012	.032	.014	.130	.100	.021
Chlorophyll c	.054	.119	.101	.399	.429	.116
Astacin carotenoids	.000	.000	.006	.027	.029	.014
Non-astacin carotenoids	.163	.212	.207	.503	.526	.214

continued

TABLE XV (continued)

Sampling Area	Depth in Feet 2.5	5	10	15	20	35
9-7-67						
Chlorophyll a	.342	.313	.201	1.167	.746	.242
Chlorophyll b	.082	.107	.051	.345	.218	.051
Chlorophyll c	.025	.100	.100	.397	.235	.080
Astacin carotenoids	.000	.000	.006	.033	.010	.011
Non-astacin carotenoids	.246	.211	.118	.542	.344	.104
Grand Marais 8-31-67						
Chlorophyll a	.633	1.723	1.895	3.513	.903	.345
Chlorophyll b	.307	.669	.424	.727	.144	.064
Chlorophyll c	.215	.714	.556	.989	.342	.095
Astacin carotenoids	.020	.002	.012	.003	.042	.006
Non-astacin carotenoids	.366	.904	.879	1.591	.380	.135
9-7-67						
Chlorophyll a	.314	1.655	1.507	2.517	1.407	.355
Chlorophyll b	.033	.176	.094	.206	.159	.019
Chlorophyll c	.048	.327	.225	.965	.583	.070
Astacin carotenoids	.000	.007	.012	.062	.046	.007
Non-astacin carotenoids	.157	.710	.621	1.021	.595	.140

TABLE XVI

PERIPHYTON DRY WEIGHTS AT STANDARD DEPTHS, NORTH SHORE STATIONS, LAKE SUPERIOR, 1967. MILLIGRAMS PER SQUARE CENTIMETER OF ROCK SURFACE

Date	Depth in Feet 2.5	5	10	15	20	35
			Lester River			
8-16	2.9	10.1	47.5	76.5	-	-
9-6	2.6	5.0	5.4	11.6	13.9	-
			Knife River			
9-5	2.8	5.0	3.6	4.3	6.8	36.3
9-15	1.1	1.1	3.5	3.2	35.8	9.8
			Burlington Bay			
8-22	7.7	3.7	13.9	20.5	-	-
9-1	17.8	9.5	35.2	19.6	22.0	-
			Split Rock River Bay			
8-29	4.8	7.6	7.6	22.6	25.1	-
9-7	7.7	9.6	13.8	9.7	14.4	14.9
			Beaver Bay			
8-29	4.5	11.0	9.4	13.1	49.8	42.8
9-14	15.1	29.9	45.4	56.4	51.8	48.6
			No-Name Bay			
9-1	4.5	2.8	13.2	3.2	4.1	-
9-14	3.6	3.3	12.6	5.7	3.5	-
			Sugar Loaf Cove			
8-31	2.0	1.9	1.7	1.5	5.5	-
9-7	3.5	1.9	4.5	2.4	2.3	-
			Tofte			
8-31	2.7	4.3	3.6	3.9	2.6	8.4
9-7	4.1	3.7	4.9	10.5	2.6	14.4
			Lutsen			
8-31	9.5	7.5	6.2	8.0	11.3	10.6
9-7	8.9	13.5	8.4	7.5	2.5	9.6
			Good Harbor Bay			
8-31	4.0	9.1	6.1	17.5	16.7	15.4
9-7	8.4	9.1	6.2	19.4	11.1	2.8
			Grand Marais			
8-31	4.9	19.3	12.9	22.2	28.6	5.8
9-7	2.1	21.7	21.1	21.9	24.7	7.8

TABLE XVII

PERIPHYTON ASH-FREE DRY WEIGHTS AT STANDARD DEPTHS, NORTH SHORE STATIONS, LAKE SUPERIOR, 1967. MILLIGRAMS PER SQUARE CENTIMETER OF ROCK SURFACE

Date	Depth in Feet 2.5	5	10	15	20	35
			Lester River			
8-16	0.38	1.23	3.33	3.54	-	-
9-6	0.90	1.25	0.63	0.91	0.95	-
			Knife River			
9-5	0.34	0.70	0.73	0.66	0.90	3.84
9-15	0.23	0.42	0.59	0.31	2.81	2.40
			Burlington Bay			
8-22	1.03	0.63	1.47	1.95	-	-
9-1	1.39	0.98	2.45	1.54	2.07	-
			Split Rock River Bay			
8-29	0.55	0.81	1.04	1.02	2.05	-
9-7	0.57	0.87	2.13	1.64	2.27	1.88
			Beaver Bay			
8-29	0.50	0.82	0.72	2.32	4.25	2.80
9-14	0.84	2.62	4.07	3.75	3.55	3.58
			No-Name Bay			
9-1	0.76	0.46	1.75	0.56	0.60	-
9-14	0.59	0.52	1.75	0.80	0.69	-
			Sugar Loaf Cove			
8-31	0.27	0.14	0.42	0.60	0.94	-
9-7	0.29	0.41	1.04	1.17	0.79	-
			Tofte			
8-31	0.43	0.72	0.66	0.89	0.57	1.24
9-7	0.76	0.82	1.14	1.80	0.50	1.95
			Lutsen			
8-31	0.49	0.49	0.27	0.65	1.22	0.91
9-7	1.43	1.89	0.97	1.14	0.39	1.13
			Good Harbor Bay			
8-31	0.53	0.97	1.16	2.44	2.67	1.32
9-7	0.81	0.98	0.67	3.21	1.85	0.59
			Grand Marais			
8-31	0.65	1.61	2.09	3.74	0.91	0.55
9-7	0.31	1.90	1.76	2.73	2.50	0.57

TABLE XVIII

PHOTOSYNTHETIC RATES, NATURALLY OCCURRING PERIPHYTON, NORTH SHORE STATIONS, LAKE SUPERIOR, 1967. MICROLITERS OF OXYGEN PER HOUR PER SQUARE CENTIMETER OF ROCK SURFACE

Date	Sampling depth in feet					
	2.5	5	10	15	20	35
			Lester River			
8-16	18.7	35.0	62.1	44.1		
			Knife River			
9-5	16.5			13.3	23.4	56.3
9-14	14.2				22.9	
			Burlington Bay			
8-22	51.8	45.0	43.4	35.8		
			Split Rock River Bay			
8-29	16.0	19.1	16.7	18.7	25.9	
9-7	47.9				14.6	
			Beaver Bay			
8-29	14.5	25.5	22.2	22.9	19.1	12.3
9-14	15.9				18.8	
			No-Name Bay			
9-14	20.3				22.2	
			Sugar Loaf Cove			
9-7	18.8				15.2	
			Tofte			
9-7	19.4				17.2	
			Lutsen			
9-7	69.7				16.8	
			Good Harbor Bay			
8-31	15.6	22.8	19.5	35.4	19.1	24.1
9-7	41.8				24.8	
			Grand Marais			
8-31	28.4	106.7	101.0	294.5	39.2	7.5
9-7	38.2				69.8	

TABLE XIX

WATER TEMPERATURES AT THE SURFACE AND THE BOTTOM AT THE STANDARD SAMPLING DEPTHS, NORTH SHORE STATIONS, LAKE SUPERIOR, 1967. DEGREES CENTIGRADE

Date	Depth in Feet						
	0.5	2.5	5	10	15	20	35
				Lester River			
8-16	21.5	21.5	20.0	9.0	8.0	-	-
9-6	23.0	22.5	21.0	20.0	11.0	9.0	-
				Knife River			
9-5	15.0	15.0	14.5	14.0	11.0	6.0	6.0
9-15	15.5	15.5	14.5	14.0	8.0	7.5	7.0
				Burlington Bay			
8-22	13.0	13.0	12.5	12.0	10.0	-	-
9-1	13.0	13.0	13.0	13.0	13.0	13.0	-
				Split Rock River Bay			
8-29	10.0	10.0	10.0	10.0	10.0	10.0	-
9-7	8.0	8.6	8.0	7.0	6.5	6.0	-
				Beaver Bay			
8-29	8.0	6.0	7.5	7.0	6.5	5.5	5.5
9-14	12.5	12.5	12.5	12.5	12.5	12.5	8.5
				No-Name Bay			
9-1	11.0	11.0	11.0	10.5	9.5	9.5	-
9-14	13.0	13.0	13.0	13.0	13.0	13.0	-
				Sugar Loaf Cove			
8-31	7.0	7.0	6.5	6.0	6.0	5.5	-
9-7	7.5	7.5	7.5	6.5	6.5	6.1	-
				Tofte			
8-31	11.0	11.0	11.0	9.5	9.5	9.0	8.5
9-7	10.8	10.8	10.5	10.5	9.5	8.6	8.0
				Lutsen			
8-31	12.5	12.5	12.5	12.0	11.5	11.5	10.0
9-7	13.0	13.0	12.5	12.5	10.0	10.0	9.0
				Good Harbor Bay			
8-31	11.5	11.5	11.0	9.0	8.5	8.6	7.8
9-7	11.5	11.5	11.0	10.0	10.0	9.5	9.5
				Grand Marais			
8-31	9.5	9.5	9.5	9.0	9.0	8.5	8.5
9-7	10.5	10.5	10.0	10.0	10.0	9.2	9.0

the periphyton in the cove, 0.143, indicated that diatoms dominated that community to an even greater extent than in Stony Point Bay. Only two other sampling areas, Tofte and No-Name Bay, supported significantly less periphyton biomass than Stony Point Bay, as indicated by pigment concentrations.

The pigment concentrations, on a unit area basis, were considerably higher at both Lester River and Grand Marais than at Stony Point Bay. In addition, a relatively high ratio of chlorophyll b/chlorophyll c at these stations indicated the presence of a substantial percentage of green algae in the periphyton. The ratios of chlorophyll b/c at Lester River (0.568) and Grand Marais (0.588) were much higher than the ratio at Stony Point Bay (0.366). Microscopic examination of samples revealed that the Lester River station was the only area which supported the growth of Cladophora, and that a rather heavy crop of Ulothrix was present at Grand Marais. Since only the Lester River and Grand Marais stations are near relatively large population centers, it is possible that local sewage effluents were partially responsible for the support of more extensive and more varied periphyton communities at these stations than in the other areas. The relatively high water temperature at the Lester River station probably contributed in large measure to the moderately heavy growth of Cladophora. According to Neil and Owen (1964), the growth of Cladophora has reached nuisance proportions in Lake Erie and Lake Ontario. The present study has shown that green algae are of minor importance in the periphyton communities of the western arm of Lake Superior. Even at the Lester River and Grand Marais stations, diatoms are the dominant algal type among the attached algae.

The dry and ash-free dry weights of the north shore periphyton were quite variable. The number of samples taken was not sufficient to allow the correlation of the weights with other parameters of biomass. The samples from Beaver Bay contained small (ten to twenty microns) black magnetic particles which adhered to the periphyton mass on the rocks. Although the total pigment concentration, on a unit area basis, in the periphyton of Beaver Bay was less than the average value for all the north shore stations, the dry weight was the highest encountered anywhere.

The gross production rates at the north shore stations, as measured by respirometry under standard conditions, were similar to those exhibited by the periphyton of Stony Point Bay. The average photosynthetic rate for organisms from a depth of 2.5 feet at all stations, 32.3 microliters of oxygen/hour/cm^2, was lower than that recorded at Stony Point Bay (44.6 microliters O_2/hour/cm^2); however, the samples from a depth of twenty feet produced 26.4 microliters O_2/hour/cm^2, compared with 19.2 microliters O_2/hour/cm^2 for the twenty foot samples from Stony Point Bay.

The types and numbers of organisms comprising the periphyton are not drastically different at any point along the 107 mile segment of the north shore of Lake Superior. Stony Point Bay would seem to qualify as a representative area for future study of the effects of changes in water quality on the condition of this community in the western arm of Lake Superior.

IV. 1968 FINDINGS

The amount of periphyton biomass along the north shore of Lake Superior was well documented by the 1967 data, and the relationships between some of the parameters used to measure the biomass were clarified as a result of the 1967 investigation. However, several questions relating to the biodynamics of this community remained.[6] Since there seemed to be an inverse relationship between light intensity and the concentration of pigments in the organisms, it was necessary to determine experimentally whether or not the concentrations would actually change if light intensity were altered. If such a change occurred, the rate of change could be measured. This factor is important in the consideration of the effects of varying turbidity in lake water on the photosynthetic activity of periphyton.

Although photosynthetic rates for the periphyton had been determined in 1967, these measurements were made under standard conditions of light intensity and temperature, and could not be applied directly to the community in the lake. It had been shown that the photosynthetic efficiency of the pigment unit under standard conditions depended on the depth from which the sample was taken. Therefore, in order to calculate the actual production rates under the variety of conditions to which the periphyton organisms are subjected, it was necessary to determine photosynthetic rates of periphyton in a crossed gradient of light intensity and temperature after the organisms had been "conditioned" to a particular set of conditions. Besides facilitating the adjustment of data collected under standard laboratory conditions in 1967, the 1968 experiments produced basic information about the effects of environmental changes on the periphyton of western Lake Superior.

Analysis of Test Communities and Water Chemistry

Periphyton samples were taken from Stony Point Bay during the summer of 1968 for "conditioning" in the laboratory. For the results of the experiments to be meaningful, it was imperative that the species composition of the samples remain constant throughout the summer. The periphyton organisms from a depth of 2.5 feet in Stony Point Bay, where most of the samples were taken for incubation, were counted and identified on nine occasions during the summer of 1968. The results of those counts (Table XX) show that the species composition of the samples remained quite constant during the period of testing. The relative numbers of the ten most predominant organisms did not vary significantly. As in previous years, the community was dominated by *Achnanthes microcephala*, *Synedra acus*, and several species of *Navicula*.

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[6] Biodynamics is defined here as that combination of internal and external factors which governs the rate and efficiency of energy transfer through a biological system.

TABLE XX

TEN MOST COMMONLY OCCURRING PERIPHYTON ORGANISMS
STONY POINT BAY, 2.5 FOOT DEPTH, 1968
NUMBER (1000's) PER SQUARE CENTIMETER OF ROCK SURFACE

Organism	Date								
	7-29	7-31	8-6	8-8	8-12	8-14	8-20	8-27	9-5
Synedra acus	1,390	1,464	1,080	1,440	1,120	946	858	880	765
Achnanthes microcephala	846	890	660	786	832	786	574	428	460
Navicula spp.	794	644	684	794	540	465	480	386	324
Cymbella spp.	166	120	104	95	144	176	145	96	92
Gomphonema spp.	72	60	66	58	46	40	58	42	38
Synedra ulna	13	6	19	10	16	5	10	12	9
Cocconeis spp.	8	10	12	14	18	12	14	8	10
Denticula thermalis	6	6	3	1	2	4	6	4	4
Fragilaria capucina	8	6	5	6	2	2	6	5	3
Amphora ovalis	2	1	4	4	1	2	1	1	1

TABLE XXI

SUMMARY OF WATER CHEMISTRY, STONY POINT BAY, 1968

Analysis	Date								
	7-29	7-31	8-6	8-8	8-12	8-14	8-20	8-27	9-5
Temperature (Degrees C.)	6.9	6.7	12.5	13.2	8.2	5.5	10.2	9.9	13.2
pH	7.76	7.69	7.88	7.84	7.86	7.85	8.07	8.15	7.88
Hardness (mg/L as $CaCO_3$)	49.3	47.5	49.7	47.4	49.4	50.8	50.8	52.3	46.0
Alkalinity (mg/L as $CaCO_3$)	43.3	42.4	41.9	42.4	43.0	42.3	42.5	43.2	42.6
Dissolved solids (mg/L)	58.0	56.0	52.2	64.5	66.5	68.6	60.6	56.4	53.7
Total Phosphorus (mg/L)	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
Nitrate Nitrogen (mg/L)	0.118	0.118	0.210	0.135	0.121	0.128	0.162	0.159	0.195
Dissolved Oxygen (mg/L)	12.7	12.5	11.3	11.2	12.4	12.6	10.9	11.3	10.5
Dissolved Oxygen (% sat.)	105	106	110	107	108	103	102	103	104
Free Carbon dioxide (mg/L)	2.10	2.20	1.30	1.45	1.62	1.70	1.00	0.85	1.29

Thus it was concluded that, for practical purposes, results of experimentation at all times during the summer were comparable and that these results could be employed for adjustment of data collected in 1967.

On one occasion, a sample was taken from Lake Superior near the mouth of the Lester River. The periphyton at this point included a large percentage of Cladophora. For the purpose of further establishing the nature of the two communities used in the experiments, photosynthetic rates were determined for samples of each at a variety of temperatures (see Figure 92). There was no sharply defined optimum temperature for photosynthesis in either community; the photosynthetic rate for the Stony Point Bay sample reached a plateau which ranged from 20° to 25° C., while the optimum rate in the sample from the Lester River station was maintained from 20° to 30° C.

Since water from Stony Point Bay was used as the medium for sustaining growth of periphyton in the incubators, it was necessary to show that the quality of the water did not change appreciably during the course of the experiments. The results of chemical analyses which were performed on the water during the summer are presented in Table XXI. Techniques described in Standard Methods for the Examination of Water and Wastewater (A.P.H.A., 1965) were employed in the chemical analysis of water samples. It is apparent that the water quality did not change significantly throughout the period of experimentation. With this fact established, it was possible to determine experimentally the effects of short-term changes in light intensity and temperature on the productivity of Lake Superior periphyton.

Relationships Between Light Intensity and Chlorophyll Concentrations

The first series of experiments was designed to demonstrate that the periphyton organisms of Stony Point Bay actually alter their concentration of chlorophyll in response to changes in light intensity, and to determine the rate at which such an alteration occurs. Six rocks supporting the growth of periphyton were taken from a depth of 2.5 feet in Stony Point Bay, where the light intensity was about 5000 foot-candles at mid-day. Six rocks were also taken from a depth of thirty-five feet, where the light intensity was about 100 foot-candles. The amount of total chlorophyll per milligram of ash-free dry weight in the 2.5 and thirty-five foot samples was shown to be 0.00571 milligrams and 0.00916 milligrams, respectively. Three of the rocks from 2.5 feet were then incubated at a light intensity of eighty foot-candles and a temperature of 10° C., while the other three were incubated at 800 foot-candles and 10° C. The rocks from the thirty-five foot depth were similarly divided and incubated under the same two sets of conditions. At two day intervals, a portion of the periphyton from each rock in each incubator was removed for pigment analysis.

The results of the pigment analyses are presented in Figure 93. The amount of chlorophyll per unit of organic weight in the periphyton which had been accustomed to a light intensity of 5000 foot-candles,

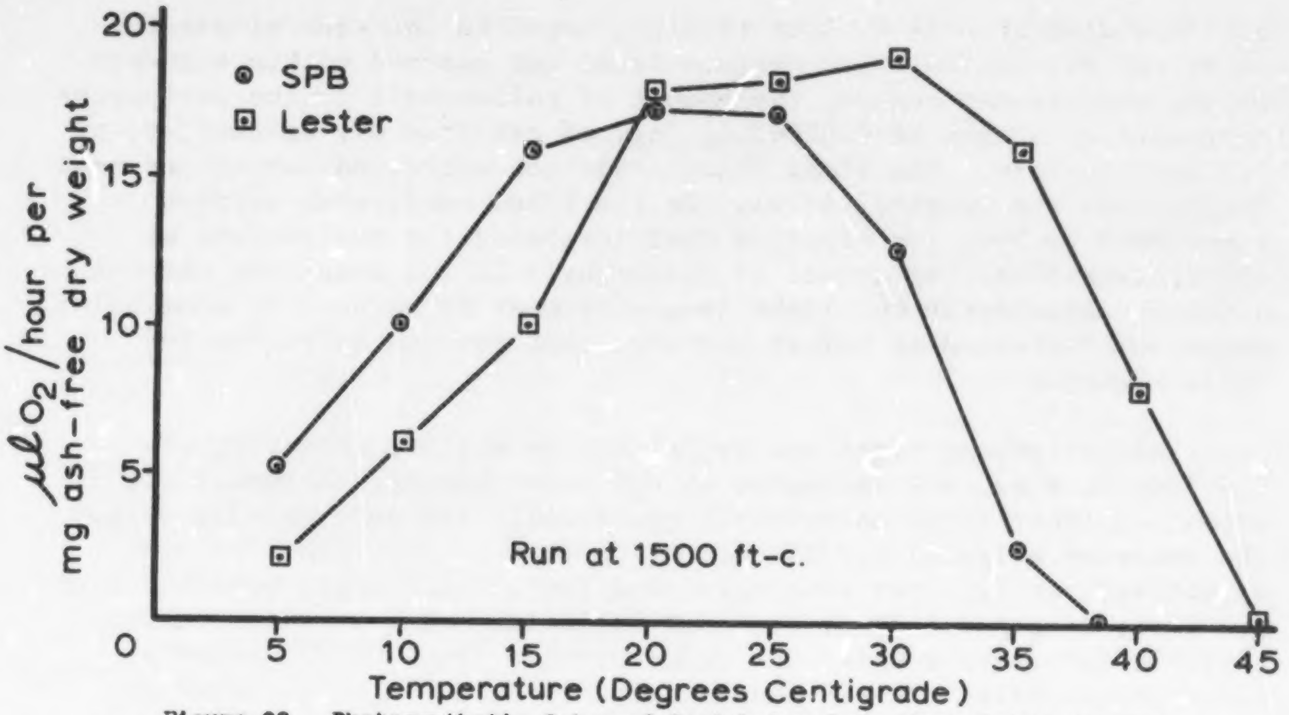

Figure 92. Photosynthetic Rates of Periphyton from Stony Point Bay and Lester River Station at Various Temperatures, June, 1968.

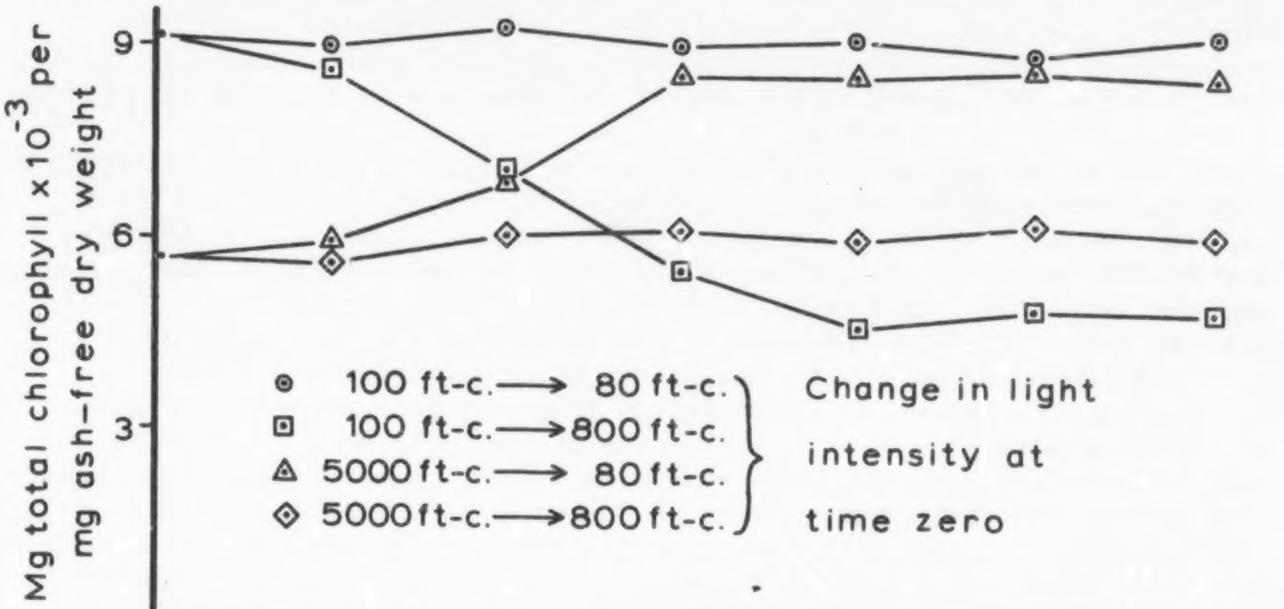

Figure 93. Change in Periphyton Chlorophyll Concentration (per unit ash-free dry weight) as Light Intensity is Severely Altered.

but incubated at only 80 foot-candles, began to increase within the first two-day period. The maximum level was reached within six days. During the six-day period, the amount of chlorophyll in the periphyton increased at a rate of 0.00043 mg./mg. of ash-free dry weight/day, or 7.5 per cent/day. The final chlorophyll concentration was 45 per cent higher than the original level. On the other hand, when samples accustomed to 5000 foot-candles were incubated for twelve days at 800 foot-candles, the amount of chlorophyll in the organisms was not altered. Apparently the light intensity must be reduced to some point below 800 foot-candles before the organisms respond by increasing their pigments.

The periphyton organisms accustomed to a light intensity of 100 foot-candles, but incubated at 800 foot-candles, decreased the amount of their total chlorophyll continually for an eight-day period. The decrease averaged 0.00058 mg. of chlorophyll/mg. ash-free dry weight/day, or 12.7 per cent/day. The final chlorophyll concentration was forty-nine per cent of the original value. The level of chlorophyll in the samples which had been switched from 100 foot-candles to 80 foot-candles did not change appreciably during the twelve-day test period.

Having established that a light intensity of less than 800 foot-candles was required to stimulate the addition of chlorophyll in the algal cells of Stony Point Bay periphyton, the next step was to determine the maximum intensity at which such an addition would be induced. For this purpose, twelve periphyton samples were taken from Stony Point Bay at a point where the mid-day light intensity was 825 foot-candles. The rocks were divided into groups of three, and the chlorophyll concentration per unit of organic dry weight was determined for each group. Each group of rocks was incubated at 10° C., but at a different light intensity (100, 250, 400 or 600 foot-candles). The amount of chlorophyll per unit of ash-free dry weight was determined for each group of samples at two-day intervals (see Figure 94). The organisms which had been subjected to a reduction in light intensity from 825 foot-candles to 100 foot-candles increased the concentration of their chlorophyll by a total of fifty-five per cent during an eight-day period, after which the concentration remained unchanged for another four days. The daily rate of increase was approximately 6.9 per cent. The samples whose light intensity had been reduced from 825 foot-candles to 250 foot-candles also increased their level of chlorophyll, but to a lesser degree than did the samples incubated at 100 foot-candles. In this case, the increase totaled thirty-six per cent, or 3.6 per cent per day over a ten-day period. The reduction from 825 to 400 foot-candles brought about a total increase in chlorophyll of eighteen per cent over an eight-day period, or 2.25 per cent per day. There was virtually no response to the decrease in light intensity from 825 to 600 foot-candles.

These experiments indicate that the light intensity must be reduced to a point somewhere between 400 and 600 foot-candles before "light-adapted" periphyton organisms will react by adding chlorophyll to their cellular material. Below 400 foot-candles, a

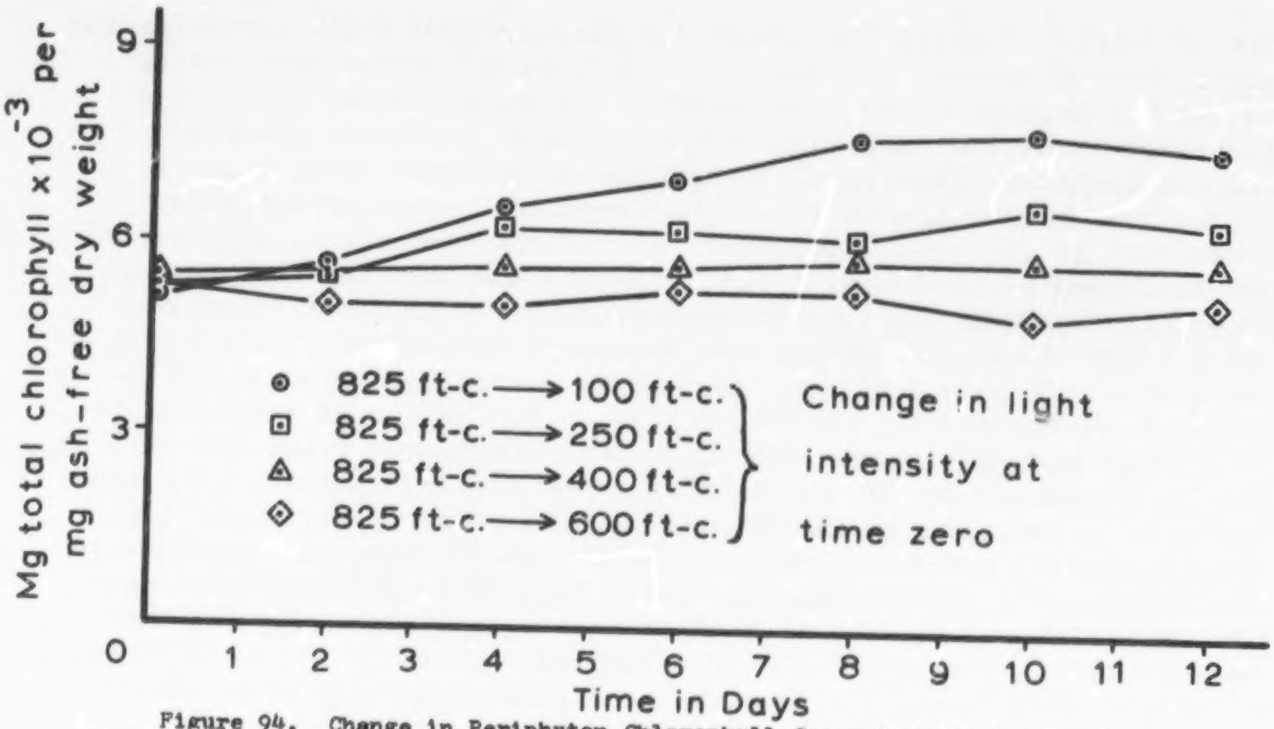

Figure 94. Change in Periphyton Chlorophyll Concentration (per unit ash-free dry weight) as Light Intensity is Moderately Altered.

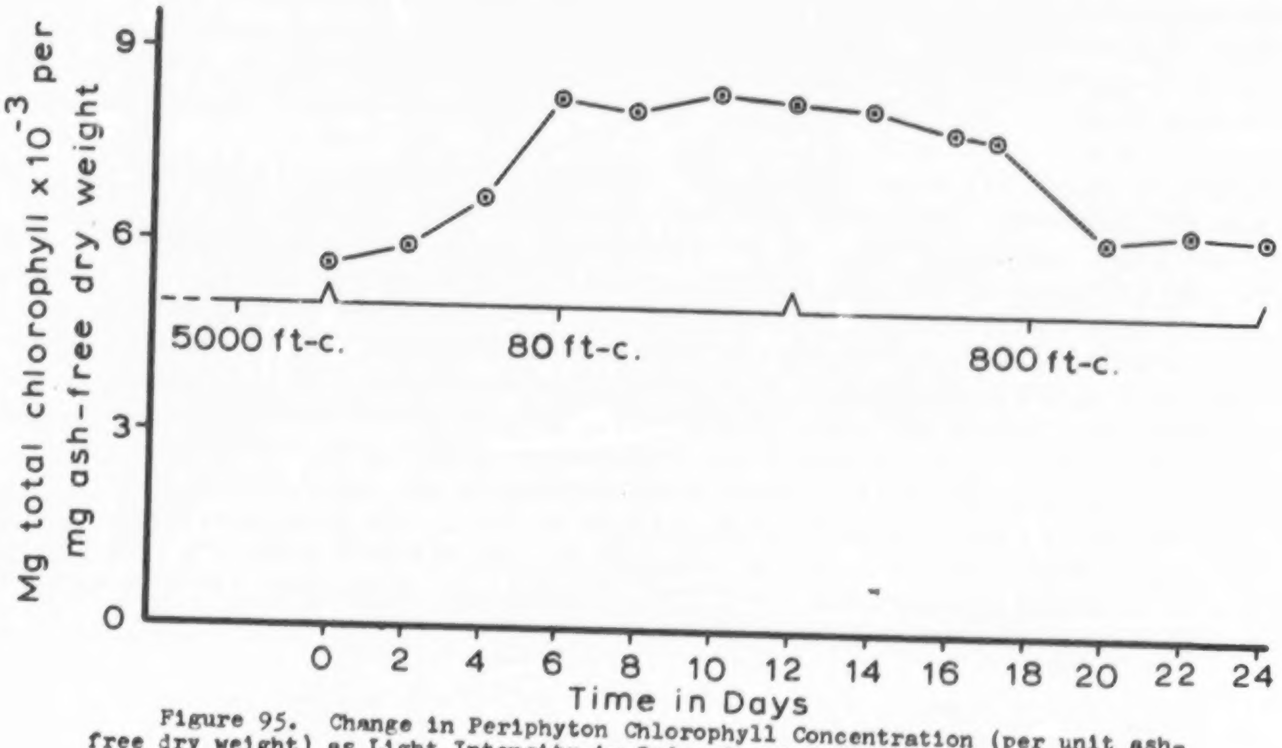

Figure 95. Change in Periphyton Chlorophyll Concentration (per unit ash-free dry weight) as Light Intensity is Reduced and Subsequently Increased.

nearly linear, inverse relationship exists between light intensity and amount of chlorophyll per unit of organic weight after equilibrium has been reached. Up to this point in the experimentation, it had been shown only that separate "light adapted" or "shade adapted" samples could be stimulated to increase or decrease their pigment concentration by changing the light intensity to which they were exposed. It was necessary to determine whether or not a single sample would respond to decreased light intensity and then to increased intensity. A sample was taken from shallow water in Stony Point Bay (about 5000 ft-c. at mid-day) and placed in an incubator at a light intensity of eighty foot-candles. After twelve days, the light intensity was changed to 800 foot-candles. The amount of total chlorophyll per unit of ash-free dry weight was determined every two days. Figure 95 shows that the chlorophyll concentration increased for about six days in response to the lowered light intensity, whereupon the concentration remained at the same level for the next six days. When the light intensity was then increased from 80 to 800 foot-candles, the amount of pigment per unit of organic weight began to fall back toward the original level. After eight days at the high light intensity, the chlorophyll level had returned to a point only slightly higher than that maintained at an intensity of 5000 foot-candles. Thus it has been shown that the periphyton respond quite rapidly to changes in light intensity (between 80 and 800 foot-candles) with virtually no lag phase in the alteration of chlorophyll concentration.

Conditioned Stony Point Bay Periphyton: Preliminary Experiment

Six rocks supporting the growth of periphyton organisms were collected from a depth of 2.5 feet in Stony Point Bay, where the light intensity at the time of sampling was about 4000 foot-candles and the temperature 15° C. A portion of this non-conditioned periphyton was removed from each rock and combined for the determination of photosynthetic rate at 15° C. and nine light intensities. The rocks were then divided into two groups and placed in the incubators. One incubator was set at a temperature of 15° C. and light intensity of 800 foot-candles; the other was set at 15° C. and 80 foot-candles. After seven days, the rocks were removed and the organisms tested for photosynthetic rate at 15° C. and nine light intensities. Figure 96 shows that conditioning at 800 foot-candles did not alter the pattern of photosynthetic rate with respect to light intensity from that exhibited by the samples accustomed to 4000 foot-candles. However, the organisms conditioned at 80 foot-candles reached light saturation at a lower intensity than did the other samples.[7] It may also be seen that the sample conditioned at 80 foot-candles produced a higher photosynthetic rate from 20 to 400 foot-candles than the other samples; on the other hand, the maximum rate for the "shade adapted" periphyton (80 ft-c.) was lower than that for the "light adapted" (800 and 4000 ft-c).

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[7] Light saturation is the point at which photosynthetic rate is no longer increased significantly in response to increased light intensity.

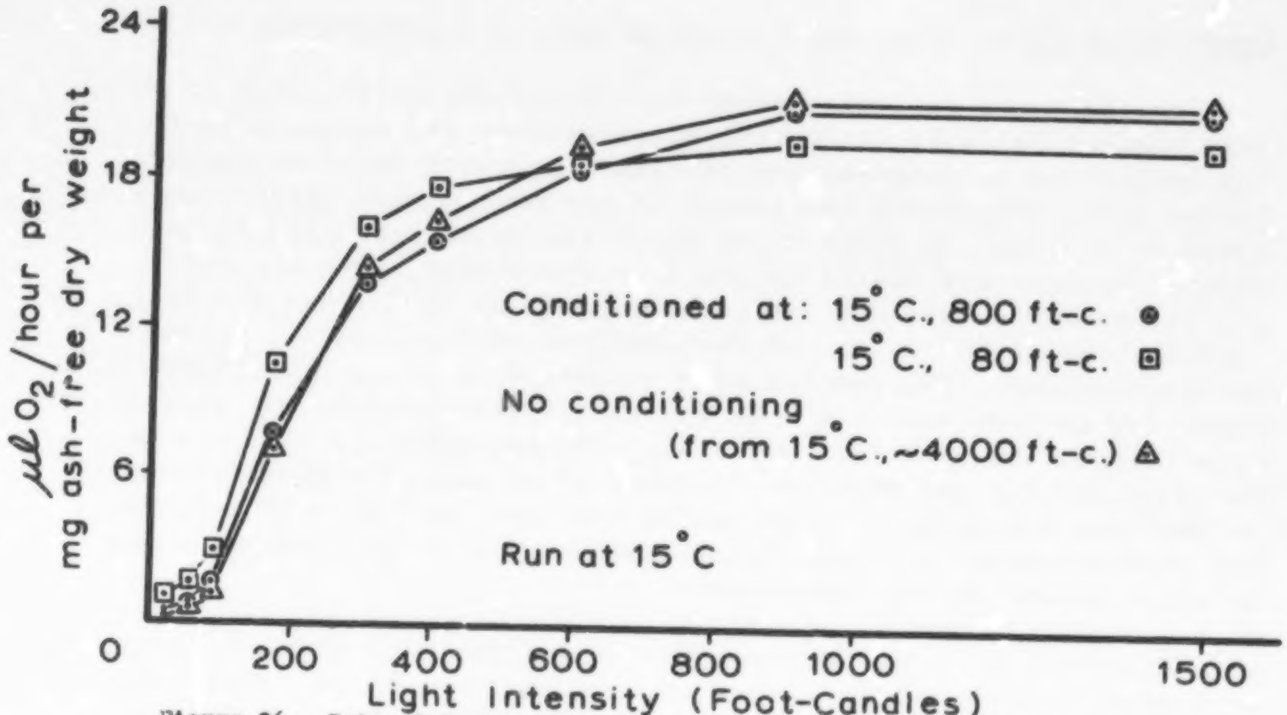

Figure 96. Rate of Photosynthesis in "Conditioned" Stony Point Bay Periphyton at Nine Light Intensities; Samples Conditioned at 80 and 800 Foot-Candles; Run at 15°C.

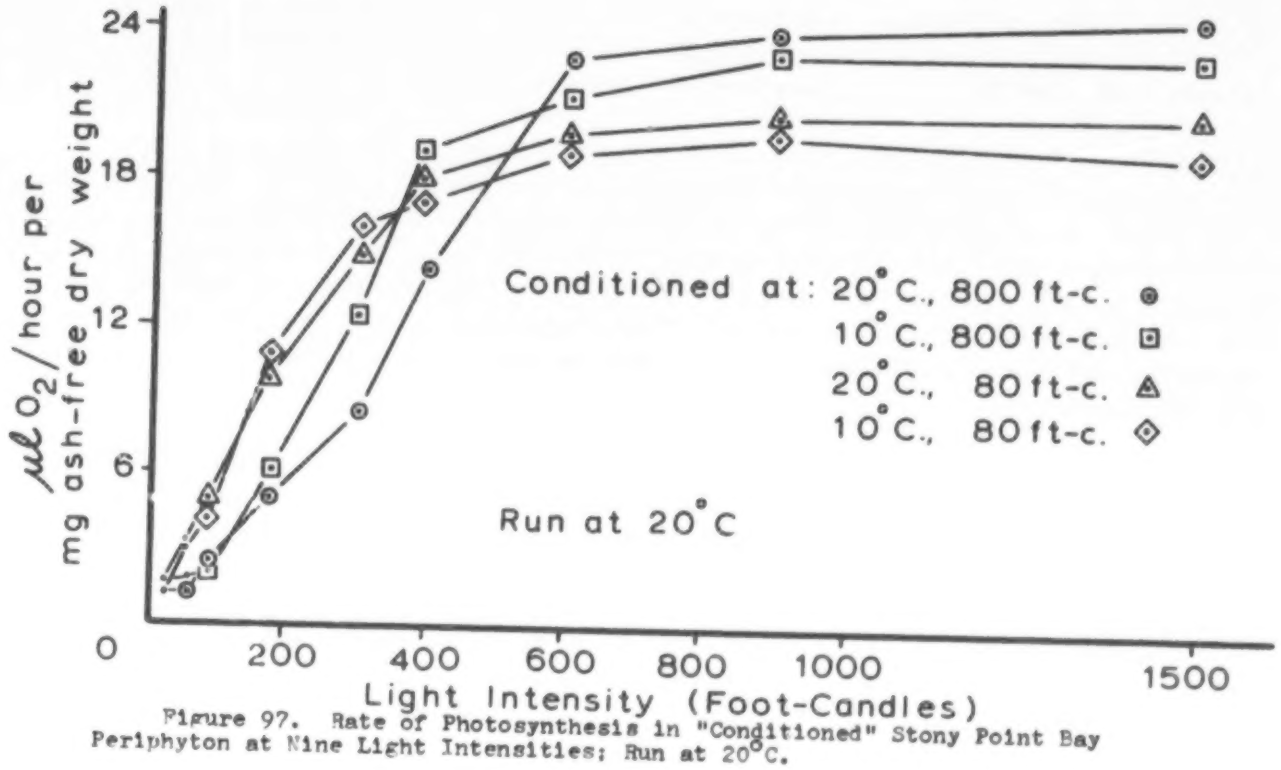

Figure 97. Rate of Photosynthesis in "Conditioned" Stony Point Bay Periphyton at Nine Light Intensities; Run at 20°C.

Conditioned Stony Point Bay Periphyton: Detailed Experiments

Having shown that the periphyton organimsms would adapt to short term changes in light intensity, an experiment was designed to test for adaptation to combinations of light intensity and temperature. Twelve rocks supporting the growth of periphyton were taken from a depth of 2.5 feet in Stony Point Bay. The rocks were divided into groups of three and placed in the four incubators. One incubator was set at 20° C. and 800 foot-candles, one at 10° C. and 800 foot-candles, one at 20° C. and 80 foot-candles, and one at 10° C. and 80 foot-candles. The samples were incubated in water from Stony Point Bay for ten days. At the end of the test period, the samples were removed and processed as usual. Pigment analyses were run on the four samples and reported in terms of amount of pigment per unit of ash-free dry weight. Aliquots of the same samples were used for the determination of gross photosynthetic rate in crossed gradients of light intensity and temperature.

The results of the photosynthetic rate determinations are presented in Figures 97 through 100. The same general pattern of "shade adapted" and "light adapted " photosynthetic rates seen in the preliminary experiment is exhibited, whether the rates were determined at 10°, 15°, or 20° C. At these temperatures, the samples conditioned at 80 foot-candles produced more oxygen at the lower light intensities than did those conditioned at 800 foot-candles regardless of the conditioning temperature. The samples conditioned at 800 foot-candles, however, reached a higher maximum rate of photosynthesis at light saturation than did those conditioned at 80 foot-candles. Slight differences due to temperature adaptation are also apparent in samples run at 10°, 15°, and 20° C. When run at 20° C. (Figure 97), the photosynthetic rate at light saturation was higher for those samples conditioned at 10° C. The reverse was true when the samples were run at 15° C. (Figure 98) and 10° C. (Figure 99). When the photosynthetic rates were determined at 5° C. (Figure 100), adaptation to temperature was more evident than adaptation to light intensity. The samples conditioned at 10° C. produced the same light-saturated photosynthetic rate at 5° C. regardless of the light intensity to which they were accustomed. Both of the samples conditioned at 10° C. exhibited a higher photosynthetic rate at all light intensities than either of the samples conditioned at 20° C. The compensation point varied somewhat for the different samples, but usually fell between 80 and 130 foot-candles.[8]

In order to illustrate another point, the same data were graphed in a different manner (Figures 101 through 104). These graphs show the effects of temperature on the production rates of each sample at

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[8] Compensation point is defined as the light intensity at which gross photosynthetic rate and respiration rate are equal (net photosynthetic rate = 0).

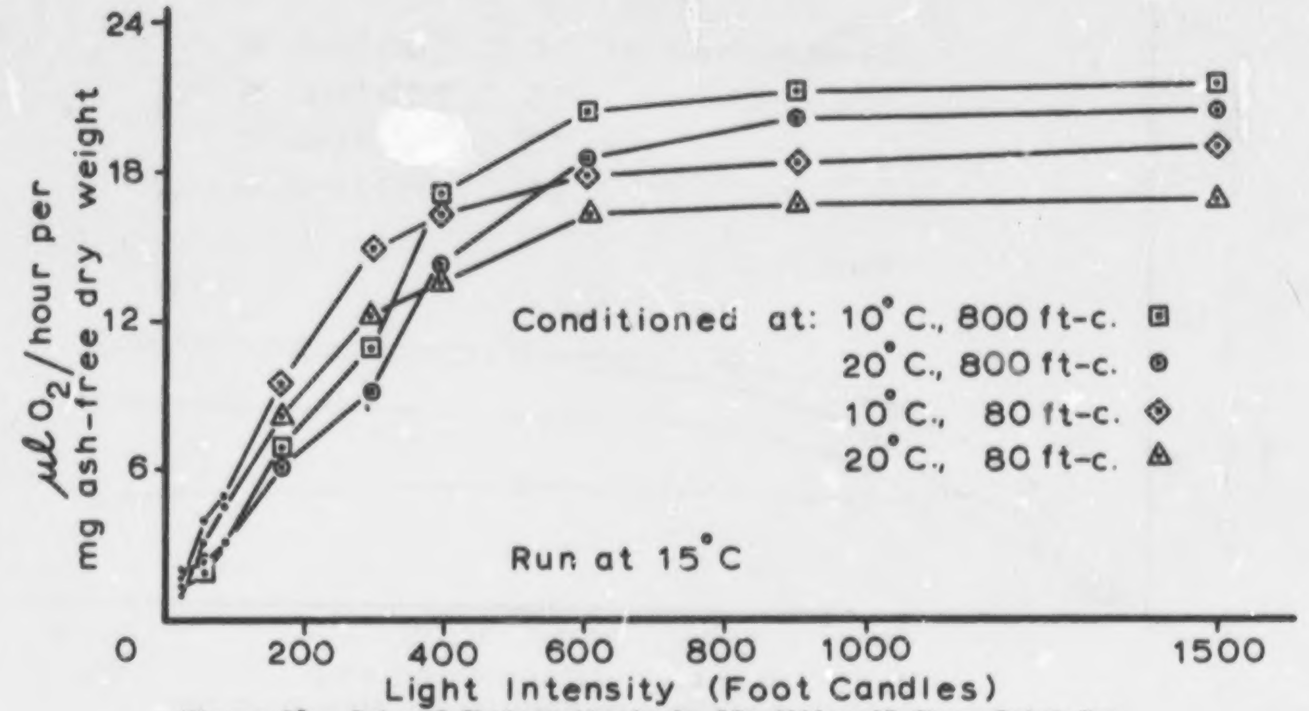

Figure 98. Rate of Photosynthesis in "Conditioned" Stony Point Bay Periphyton at Nine Light Intensities; Run at 15°C.

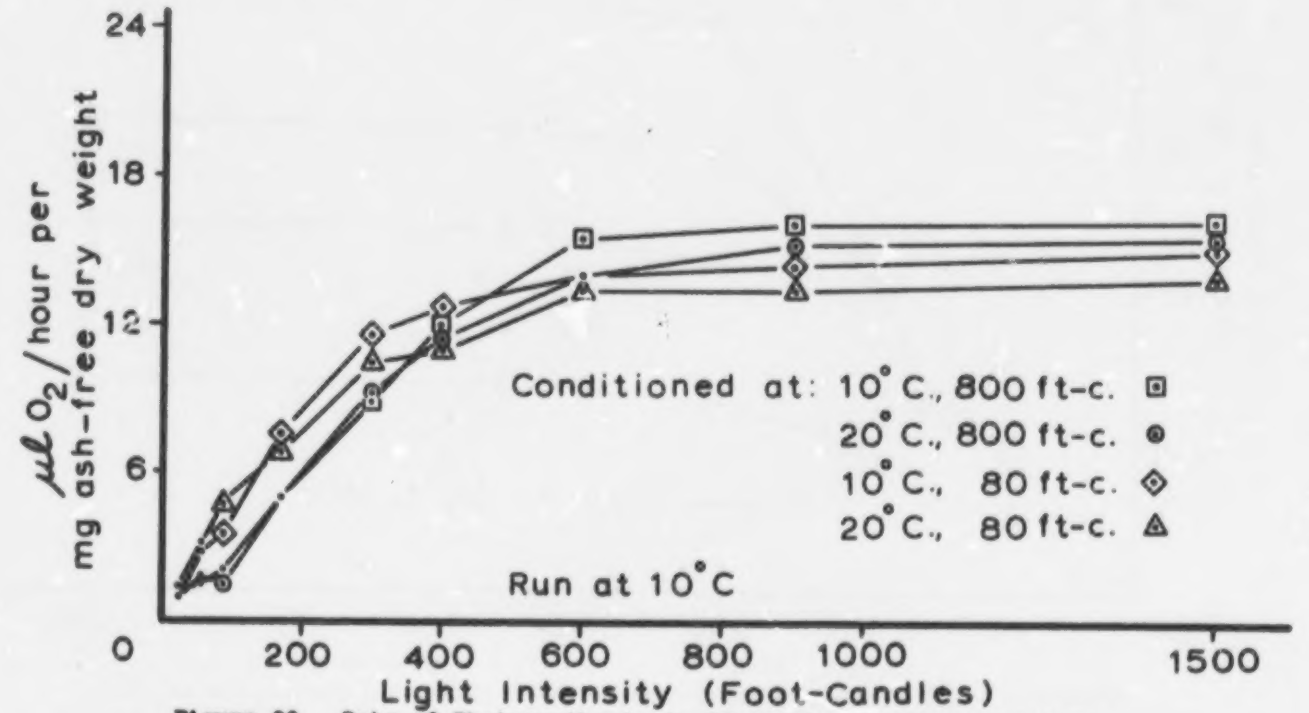

Figure 99. Rate of Photosynthesis in "Conditioned" Stony Point Bay Periphyton at Nine Light Intensities; Run at 10°C.

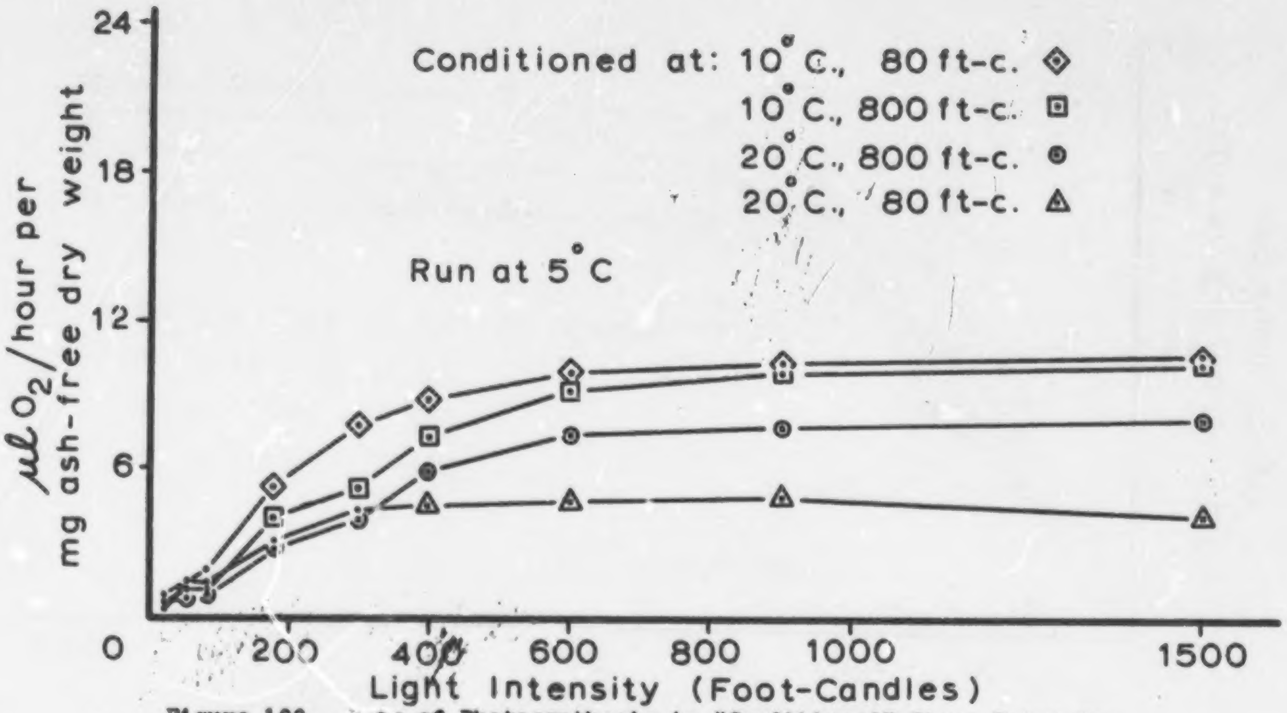

Figure 100. Rate of Photosynthesis in "Conditioned" Stony Point Bay Periphyton at Nine Light Intensities; Run at 5°C.

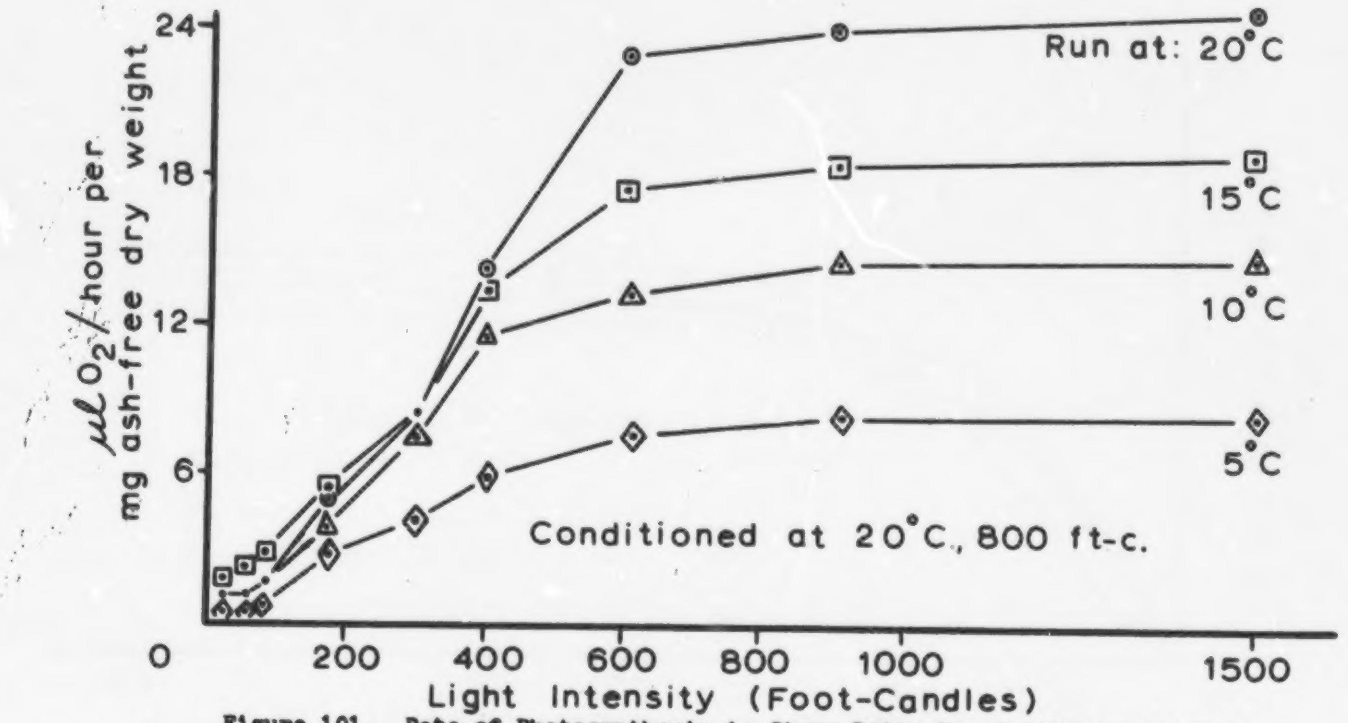

Figure 101. Rate of Photosynthesis in Stony Point Bay Periphyton at Nine Light Intensities and Four Temperatures; "Conditioned" at 20°C., 800 Foot-Candles.

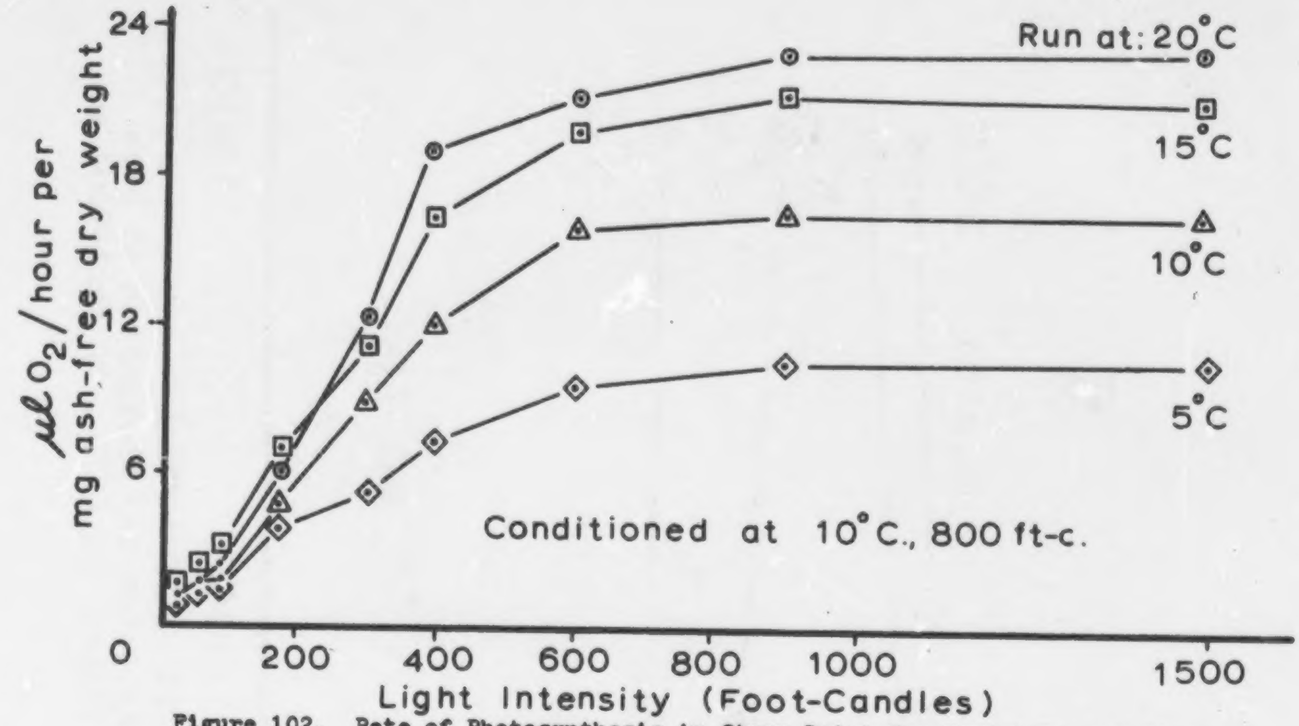

Figure 102. Rate of Photosynthesis in Stony Point Bay Periphyton at Nine Light Intensities and Four Temperatures; "Conditioned" at 10°C., 800 Foot-Candles.

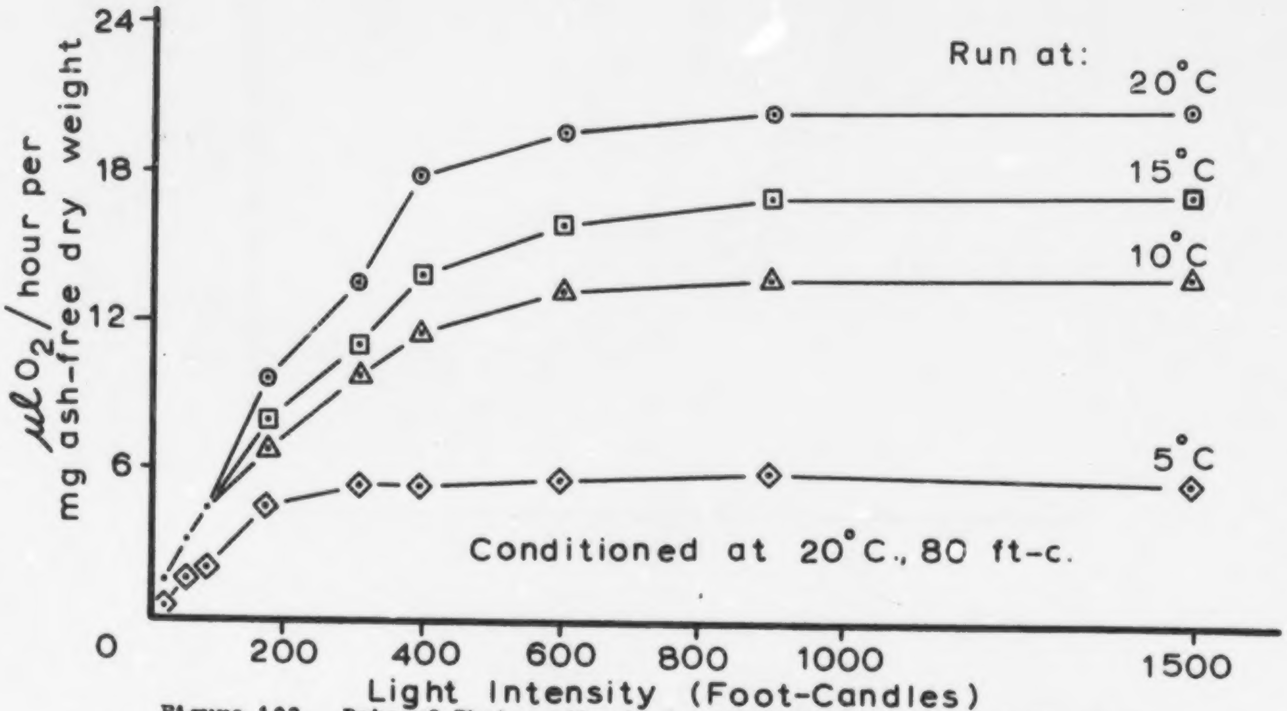

Figure 103. Rate of Photosynthesis in Stony Point Bay Periphyton at Nine Light Intensities and Four Temperatures; "Conditioned" at 20°C., 80 Foot-Candles.

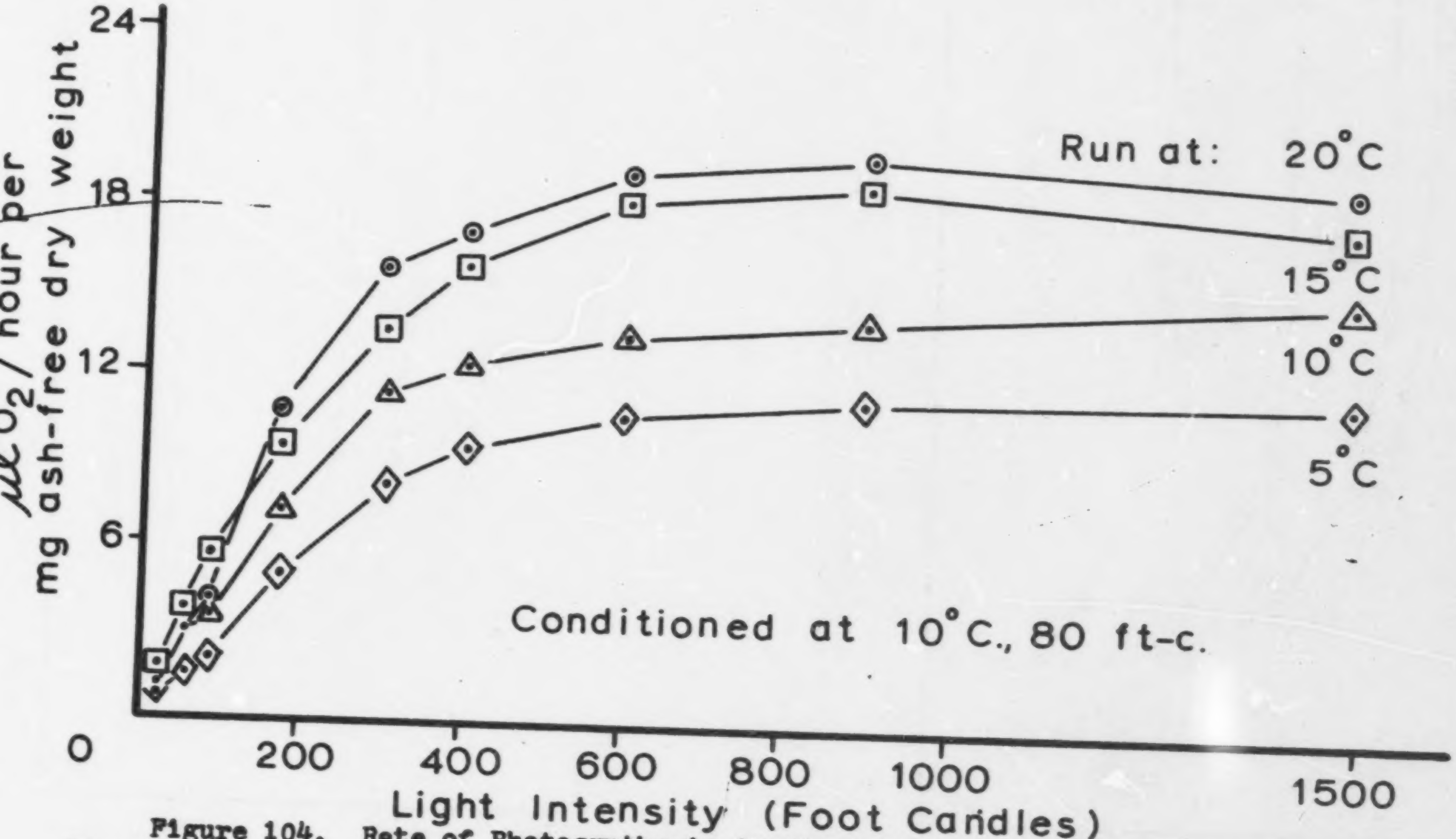

Figure 104. Rate of Photosynthesis in Stony Point Bay Periphyton at Nine Light Intensities and Four Temperatures; "Conditioned" at 10°C., 80 Foot-Candles.

the various light intensities. It is apparent that the test temperatures produced a wider spread in the photosynthetic rates in the samples incubated at 20° C. than in the ones incubated at 10° C. Samples conditioned at 20° C. produced more oxygen when run at 20° C. and less when run at 5° C. than those conditioned at 10° C. This point is emphasized by the temperature coefficients (Q_{10}) which were calculated for all of the samples (see Table XXII). Q_{10} calculated for the temperature range of 5° C. to 20° C. for samples incubated at 20° C. and 800 foot-candles was about 2.0 at light saturation; the value for samples incubated at 20° and 80 foot-candles was about 2.5 at light saturation. In contrast, Q_{10} for samples incubated at 10° C. and 800 foot-candles was approximately 1.7 at light saturation, while the value for samples incubated at 10° C. and 80 foot-candles was about 1.5. Q_{10} was also calculated for all samples at all test light intensities for three intermediate temperature ranges (5°-10° C., 10°-15° C., 15°-20° C.). These values are more variable than the ones calculated for the larger temperature range, especially at the lower light intensities.

Assimilation values were calculated for the four samples at all light intensities and temperatures (see Table XXIII). The assimilation values at all test light intensities are higher for samples incubated at 800 foot-candles than for those incubated at 80 foot-candles, regardless of temperature, even though the latter samples had more chlorophyll per unit weight. This fact confirms the suggestion, first made in 1966, that the chlorophyll unit becomes less efficient as an organism adds more chlorophyll to its cellular material.

Following the conclusion of the experiment, the entire procedure was repeated, the only difference being that the samples were collected from a depth of thirty-five feet in Stony Point Bay instead of from 2.5 feet. The purpose of the second experiment was to determine whether or not samples accustomed to relatively low light intensity and temperature would be affected by conditioning in the same manner as were those from an area of high light intensity and temperature. The results of the latter experiment are presented in Table XXIV. The photosynthetic rates measured in crossed gradients of light intensity and temperature indicate that the samples from thirty-five feet reacted to the conditioning in the same way as did the samples from 2.5 feet.

In order to determine the effects of conditioning periphyton samples at intermediate light intensities, samples were collected from a depth of fifteen feet in Stony Point Bay (825 foot-candles at mid-day; 15° C.) and incubated for ten days at 100, 250, 400, and 600 foot-candles and a temperature of 15° C. Photosynthetic rates were then determined for the four samples at nine light intensities and four temperatures. The rates are presented in Table XXV. The "shade" reaction is obvious in the rates produced by the sample which had been incubated at 100 foot-candles, as light saturation is reached at 300-400 foot-candles. This type of reaction is still present, but less obvious, in the sample incubated at 250 foot-candles. Light saturation in the sample incubated at 400 foot-

TABLE XXII

TEMPERATURE COEFFICIENTS (Q_{10}) FOR CONDITIONED PERIPHYTON FROM STONY POINT BAY, 1968

Light Intensity	Temperature range (C°)			
	5 - 10°	10 - 15°	15 - 20°	5 - 20°
Conditioned at 20°C, 800 ft-c.				
20 ft-c.	5.40	2.04	-2.04	1.76
60	2.56	2.62	-2.62	1.37
80	3.06	2.04	-2.04	1.45
180	2.74	1.56	-1.18	1.53
300	3.61	1.25	0	1.65
400	3.84	1.37	1.23	1.87
600	2.82	1.66	1.82	2.06
900	2.82	1.72	1.58	1.97
1500	2.95	1.64	1.59	1.98
Conditioned at 10°C, 800 ft-c.				
20 ft-c.	4.00	1.56	-1.56	1.59
60	2.02	2.16	-2.16	1.26
80	1.46	2.46	-2.00	1.27
180	1.93	1.96	1.37	1.41
300	2.89	1.66	1.30	1.84
400	2.56	1.88	1.32	1.86
600	2.49	1.72	1.25	1.75
900	2.31	1.72	1.17	1.66
1500	2.31	1.72	1.21	1.69
Conditioned at 20°C, 80 ft-c.				
20 ft-c.	12.25	0	0	2.31
60	4.58	0	0	1.66
80	7.84	0	0	1.99
180	5.42	1.39	1.39	2.21
300	3.42	1.30	1.56	1.92
400	6.15	1.39	1.72	2.46
600	6.76	1.44	1.56	2.48
900	5.52	1.44	1.53	2.31
1500	7.12	1.39	1.53	2.48
Conditioned at 10°C, 80 ft-c.				
20 ft-c.	1.89	2.68	-2.68	1.24
60	3.45	1.85	-1.85	1.52
80	2.89	1.90	-1.39	1.59
180	2.31	1.56	1.21	1.64
300	1.79	1.59	1.35	1.53
400	1.82	1.77	1.10	1.53
600	1.82	1.61	1.12	1.50
900	1.69	1.72	1.10	1.48
1500	1.93	1.49	1.12	1.48

TABLE XXIII

ASSIMILATION VALUES FOR CONDITIONED PERIPHYTON FROM STONY POINT BAY, 1968 GRAMS OF CARBON FIXED PER GRAM OF CHLOROPHYLL

Light Intensity	Temperature			
	5°C	10°C	15°C	20°C
Conditioned at 20°C, 800 ft-c.				
20 ft-c.	0.06	0.14	0.21	0.14
60	0.10	0.16	0.27	0.16
80	0.12	0.22	0.31	0.22
180	0.29	0.49	0.62	0.57
300	0.39	0.78	0.84	0.84
400	0.62	1.22	1.43	1.58
600	0.83	1.39	1.81	2.45
900	0.92	1.55	2.02	2.59
1500	0.93	1.60	2.06	2.59
Conditioned at 10°C, 800 ft-c.				
20 ft-c.	0.07	0.14	0.17	0.14
60	0.14	0.19	0.29	0.19
80	0.16	0.19	0.35	0.23
180	0.42	0.56	0.82	0.70
300	0.55	0.88	1.11	1.23
400	0.87	1.40	1.92	2.22
600	1.11	1.75	2.30	2.57
900	1.23	1.87	2.44	2.63
1500	1.23	1.87	2.44	2.63
Conditioned at 20°C, 80 ft-c.				
20 ft-c.	0.02	0.08	0.08	0.05
60	0.08	0.15	0.17	0.17
80	0.09	0.25	0.25	0.25
180	0.17	0.40	0.46	0.55
300	0.22	0.49	0.59	0.76
400	0.26	0.64	0.75	0.99
600	0.28	0.73	0.87	1.09
900	0.32	0.75	0.90	1.12
1500	0.28	0.76	0.90	1.12
Conditioned at 10°C, 80 ft-c.				
20 ft-c.	0.04	0.05	0.08	0.05
60	0.07	0.12	0.17	0.12
80	0.09	0.15	0.21	0.18
180	0.22	0.34	0.42	0.47
300	0.31	0.45	0.57	0.65
400	0.40	0.54	0.72	0.76
600	0.45	0.60	0.77	0.82
900	0.48	0.62	0.81	0.86
1500	0.48	0.67	0.82	0.87

TABLE XXIV

PHOTOSYNTHETIC RATES OF CONDITIONED PERIPHYTON FROM THIRTY-FIVE FOOT DEPTH, STONY POINT BAY, 1968 MICROLITERS OF OXYGEN PER HOUR PER MILLIGRAM ASH-FREE DRY WEIGHT

Light Intensity	Temperature			
	5°C	10°C	15°C	20°C
Conditioned at 20°C, 800 ft-c.				
20 ft-c.	0.6	1.5	2.2	1.6
60	1.1	1.7	2.8	1.8
80	1.3	2.2	3.2	2.4
180	3.0	5.0	6.8	6.0
300	4.0	9.0	9.8	9.5
400	6.4	13.4	14.6	16.6
600	8.8	15.5	20.3	24.8
900	9.4	16.0	21.4	26.0
1500	9.2	15.0	21.4	25.8
Conditioned at 10°C, 800 ft-c.				
20 ft-c.	0.8	1.1	1.6	1.1
60	1.4	1.8	2.8	1.6
80	1.7	2.2	3.2	2.0
180	4.0	5.4	8.0	6.2
300	5.6	9.0	10.8	11.0
400	8.8	13.9	18.0	20.2
600	9.8	17.8	21.6	23.5
900	10.8	17.8	22.4	24.6
1500	10.8	18.0	22.4	24.6
Conditioned at 20°C, 80 ft-c.				
20 ft-c.	0.6	1.4	1.6	1.4
60	1.8	3.2	3.4	3.2
80	2.1	5.0	5.6	5.0
180	4.6	8.4	10.0	10.5
300	5.8	10.6	12.5	15.4
400	6.4	13.0	15.0	19.6
600	7.0	15.8	17.0	20.6
900	7.6	16.8	18.2	23.0
1500	7.4	16.4	18.6	23.0
Conditioned at 10°C, 80 ft-c.				
20 ft-c.	1.0	1.2	1.9	1.2
60	1.6	2.9	3.9	2.8
80	2.2	3.6	5.0	4.5
180	4.9	8.1	10.2	11.3
300	7.0	11.0	14.5	16.0
400	8.5	13.0	18.6	19.5
600	9.5	15.8	18.5	20.0
900	9.5	16.0	19.5	22.5
1500	9.4	16.1	19.5	22.5

TABLE XXV

PHOTOSYNTHETIC RATES OF STONY POINT BAY PERIPHYTON CONDITIONED AT INTERMEDIATE LIGHT INTENSITIES MICROLITERS OF OXYGEN PER HOUR PER MILLIGRAM ASH-FREE DRY WEIGHT

Light Intensity	Temperature			
	5°C	10°C	15°C	20°C
Unconditioned sample (from 15°C, 825 ft-c.)				
20 ft-c.	0.5	0.5	0.5	0.6
60	0.5	0.8	0.9	1.3
80	0.8	1.0	1.2	2.3
180	1.9	3.1	3.4	4.9
300	3.2	4.9	5.8	8.6
400	7.8	8.9	10.0	14.9
600	10.9	11.9	13.7	17.5
900	10.9	12.8	15.4	17.8
1500	11.0	12.8	15.5	18.0
Conditioned at 15°C, 600 ft-c.				
20 ft-c.	0.5	0.6	0.5	0.8
60	0.8	0.8	0.9	1.0
80	1.0	1.0	1.2	2.0
180	2.0	2.6	3.4	5.8
300	3.8	4.1	5.8	8.9
400	6.8	7.1	10.0	15.2
600	9.5	11.0	13.7	16.4
900	10.2	12.2	14.8	17.0
1500	10.2	12.4	15.0	17.1
Conditioned at 15°C, 400 ft-c.				
20 ft-c.	0.6	0.6	0.7	0.8
60	1.0	0.8	1.2	1.2
80	1.2	1.2	1.6	1.8
180	2.3	3.6	4.0	5.1
300	4.6	6.8	8.0	9.8
400	6.2	8.4	11.8	13.3
600	8.8	11.0	13.4	15.9
900	9.0	11.8	14.0	16.3
1500	9.2	11.8	14.3	16.5
Conditioned at 15°C, 250 ft-c.				
20 ft-c.	0.6	0.6	0.7	0.9
60	1.0	1.0	1.2	1.4
80	1.2	1.4	1.6	3.0
180	3.6	4.5	6.6	8.5
300	6.8	7.4	8.8	11.2
400	8.4	10.9	12.3	14.9
600	9.0	11.6	13.2	16.5
900	9.0	11.6	13.8	16.6
1500	9.0	11.9	14.0	16.5
Conditioned at 15°C, 100 ft-c.				
20 ft-c.	0.4	0.6	0.9	0.9
60	0.4	0.9	1.4	1.5
80	0.9	1.6	2.2	2.8
180	3.6	6.2	8.0	9.1
300	5.4	7.8	10.1	12.0
400	7.2	8.1	11.1	13.6
600	7.8	8.9	11.5	13.8
900	7.8	9.6	12.0	14.0
1500	8.0	9.8	12.2	14.1

candles is reached at about 600 foot-candles. The curve produced by plotting photosynthetic rate against light intensity for the sample incubated at 600 foot-candles nearly paralleled that of the original "light adapted" sample.

Since the periphyton community at the Lester River station in Lake Superior was one of the few which differed significantly from the community at Stony Point Bay, photosynthetic rates of a "non-conditioned" sample from that station were determined in crossed gradients of light intensity and temperature. The temperature at the sampling point was 21° C., and the light intensity was about 4500 foot-candles. The purpose was to see whether or not the rates for a community rich in Cladophora would differ from those of the diatom community of Stony Point Bay. The results of this experiment are shown in Figure 105. The general magnitude of the photosynthetic rates, expressed as microliters of oxygen produced per milligram of ash-free dry weight, was very similar to that exhibited by the samples from Stony Point Bay. The slope of the curves was typical of the "light adapted" reaction, and light saturation was reached at about 900 foot-candles.

Photosynthetic Rates of Non-conditioned Stony Point Bay Periphyton

Several samples of Stony Point Bay periphyton were collected from the six standard sampling depths during the summer of 1968 for analysis of photosynthetic rates at various light intensities. One such group of samples was taken on August 9, following a ten-day period of very clear weather. During that period, there was little wave action and very low turbidity in Stony Point Bay. The light intensities at the six standard depths when the samples were taken were as follows:

2.5' - 5250 foot-candles
5' - 4250
10' - 2330
15' - 910
20' - 475
35' - 250

The photosynthetic rates of these samples at nine light intensities are shown in Figure 106. There is little difference in the curves for the samples from 2.5, 5, 10, and 15 feet. These curves are typical of the "light adapted" reaction; light saturation was reached at about 600 foot-candles. The thirty-five foot sample produced photosynthetic rates which were typical of the "shade adapted" reaction, reaching light saturation at about 400 foot-candles. At all intensities below 600 foot-candles, the thirty-five foot sample produced more oxygen per unit of organic weight than the other samples. Above 600 foot-candles, however, it produced less than the others. A hint of the "shade" reaction was exhibited by the sample from twenty feet.

Another group of samples was taken on August 22. During the period between August 13 and August 22, the weather was cloudy and

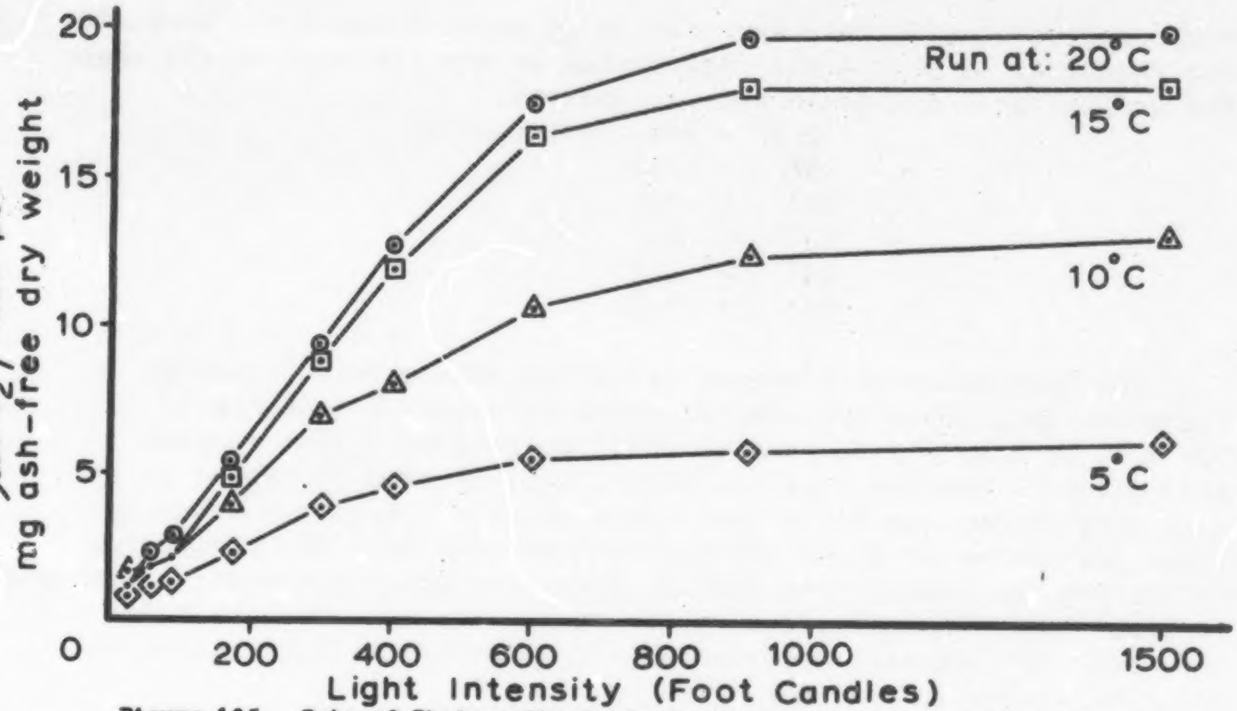

Figure 105. Rate of Photosynthesis in Periphyton from Lester River Station (Lake Superior) at Nine Light Intensities and Four Temperatures.

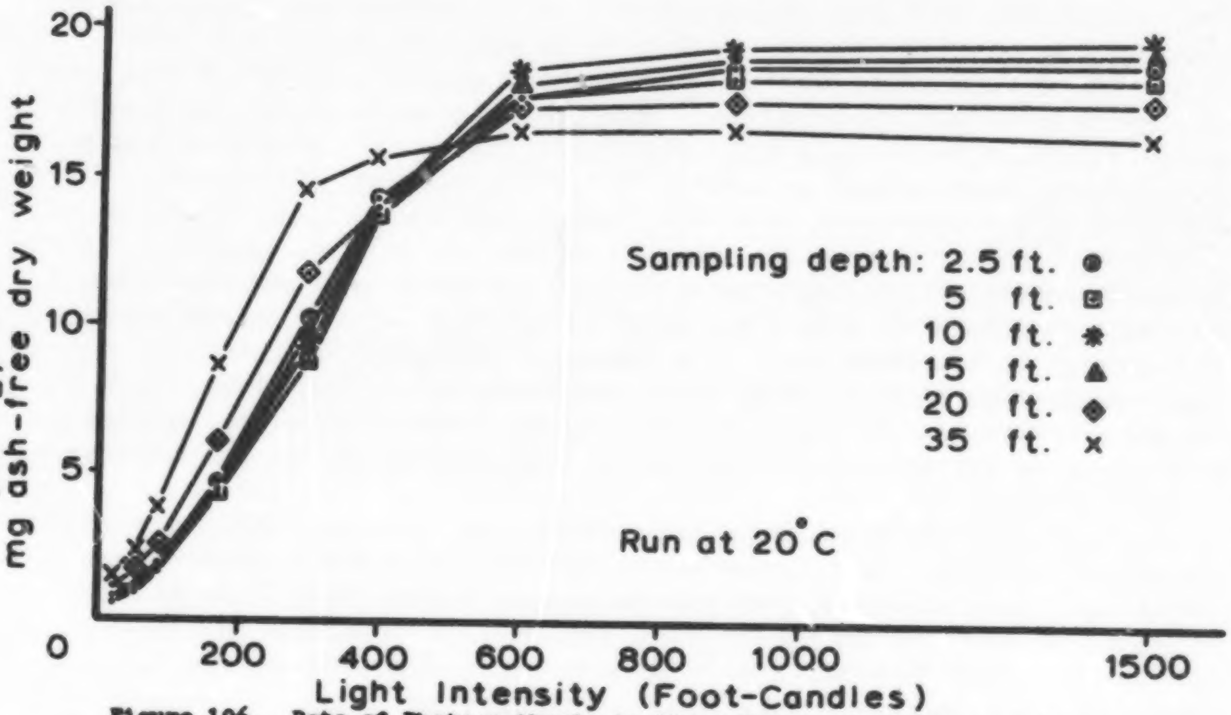

Figure 106. Rate of Photosynthesis in Stony Point Bay Periphyton from Standard Depths Following Period of Clear Weather; Run at Nine Light Intensities.

winds caused considerable wave action in Stony Point Bay. Turbidity was relatively high. Light intensities at the standard depths when the samples were collected were as follows:

2.5' - 2440 foot-candles
5' - 1250
10' - 950
15' - 325
20' - 225
35' - 105

Photosynthetic rate curves for these samples were somewhat different than those for samples taken on August 9 (see Figure 107). The 2.5, 5, and 10 foot samples still reacted as "light adapted" communities. However, the curves for samples from all three of the remaining depths exhibited the "shade adapted" reaction, reaching light saturation at about 300 to 400 foot-candles. The periphyton at fifteen and twenty foot depths in the bay were presumably conditioned to lower light intensity during the stormy period. These results show that the adaptations which were induced in the laboratory can occur naturally in the lake.

Diurnal Variation in Respiration Rate

For the purpose of calculating daily net production rates from the 1967 periphyton data, it was assumed that the respiration rate remained constant throughout a twenty-four hour period. To test this assumption, a sample from the 2.5 foot depth in Stony Point Bay was tested for respiration rate in the dark at hourly intervals for twenty-four hours. Net photosynthetic rate during alternate light periods was also determined each hour. Gross photosynthetic rate was calculated from net photosynthesis and respiration measurements. The results of these hourly measurements are presented in Figure 108. The net photosynthetic rate remained quite constant during the entire twenty-four hour period. However, the respiration rate and gross photosynthetic rate both decreased during the nighttime hours, reaching minimum values at about 4:00 A.M. Between 10:00 P.M. and 7:00 A.M., the rates averaged lower than the daytime readings by about 2.5 microliters of oxygen/hour/mg. of organic weight. The diurnal reduction in respiration should be taken into account when net daily production rates are calculated from instantaneous rates determined in the daytime. As a point of academic interest, this experiment demonstrated that gross photosynthetic rate should not be measured in artificial light during the nighttime hours, because that rate is not a true reflection of photosynthesis in the daytime.

On another occasion, the same experiment was run using a sample of Stony Point Bay periphyton which had been incubated in constant light (800 foot-candles) for ten days (see Figure 109). In this case, no diurnal variation in respiration rate appeared during the twenty-four hour period. It is assumed that the long period of constant light destroyed the respiratory rhythm.

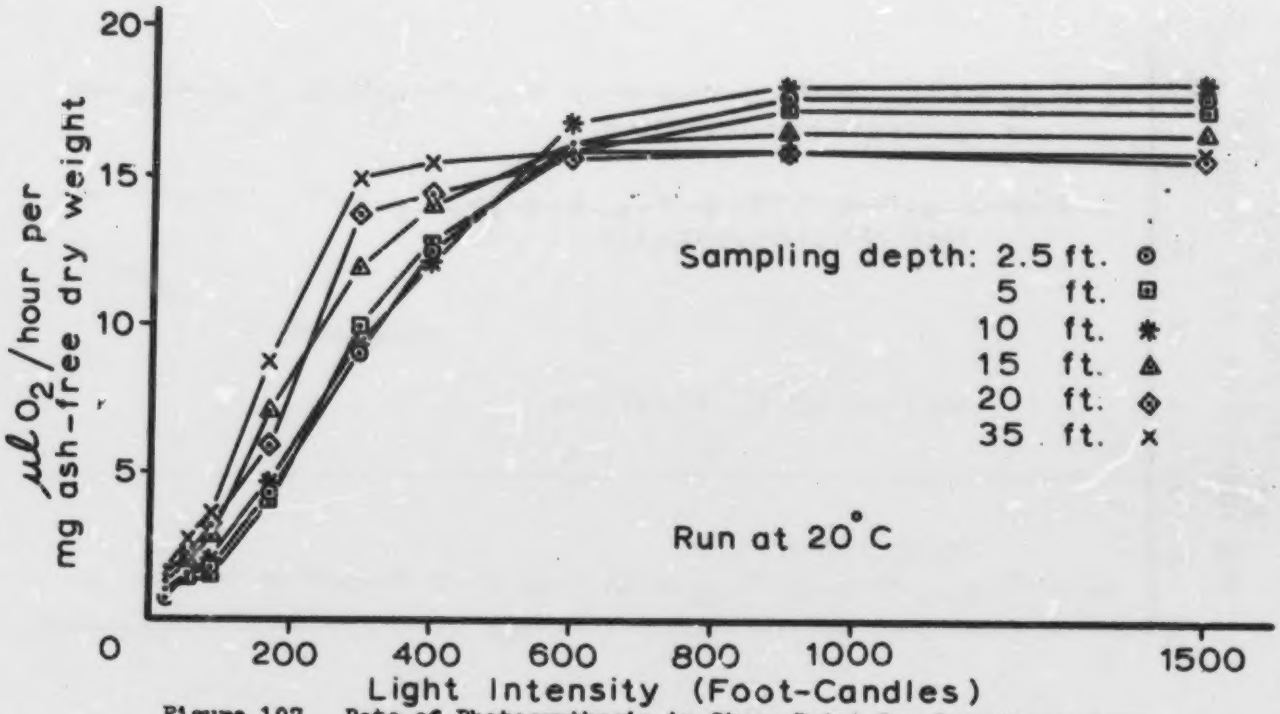

Figure 107. Rate of Photosynthesis in Stony Point Bay Periphyton from Standard Depths Following Period of Stormy Weather; Run at Nine Light Intensities.

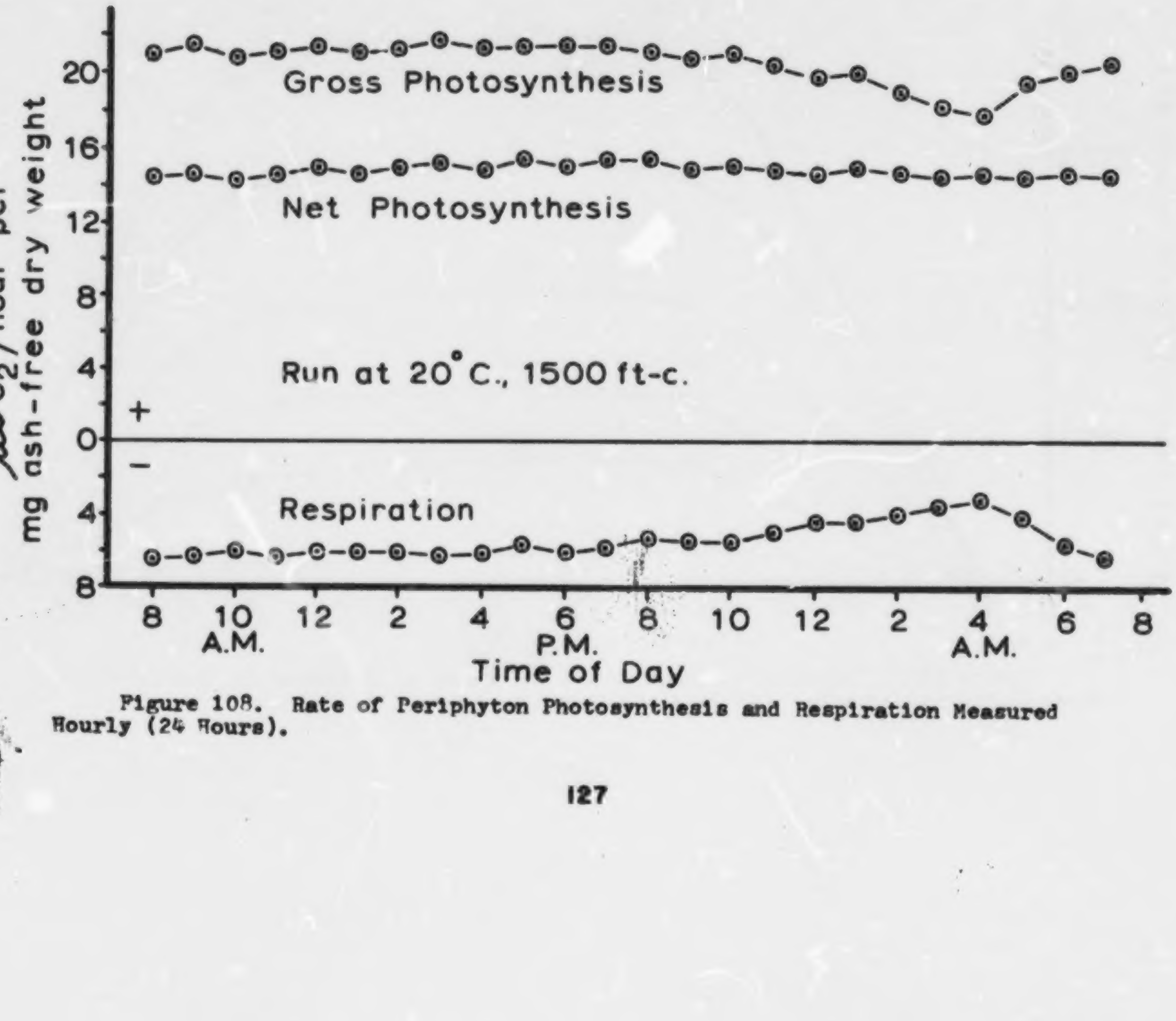

Figure 108. Rate of Periphyton Photosynthesis and Respiration Measured Hourly (24 Hours).

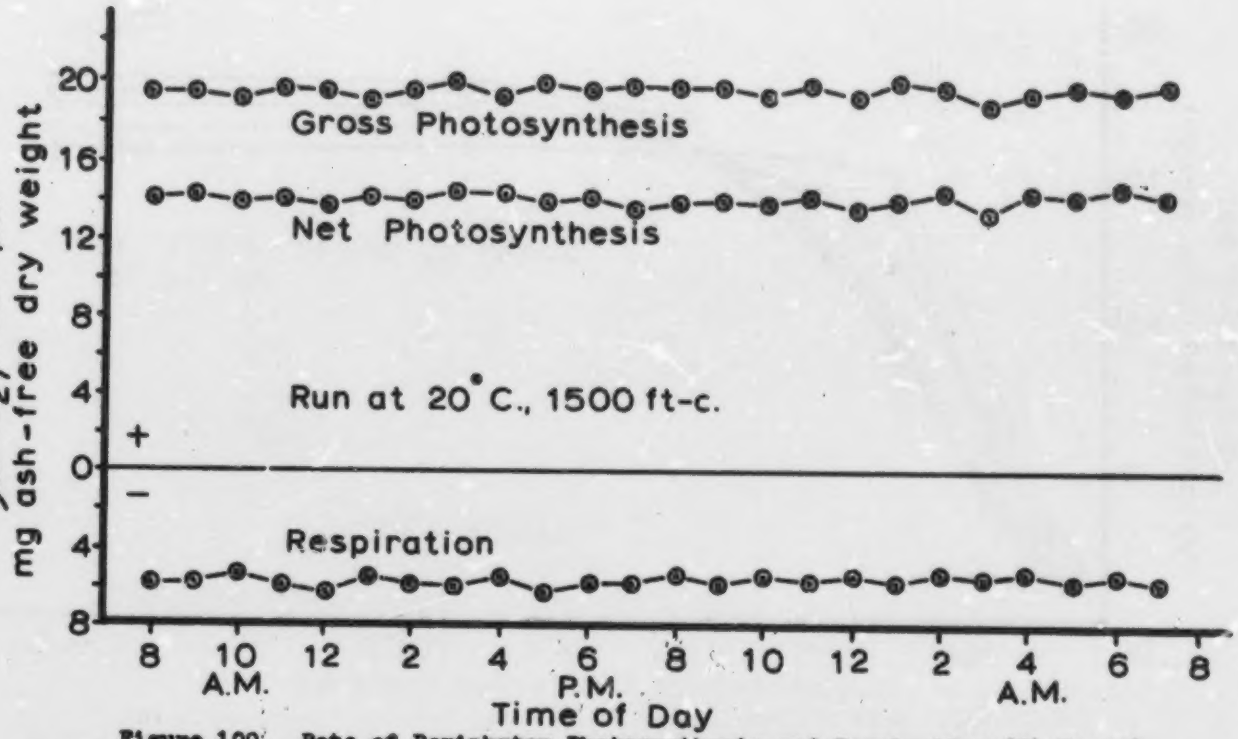

Figure 109. Rate of Periphyton Photosynthesis and Respiration (24 Hours) Following Ten-Day Period of Incubation in Continuous Light.

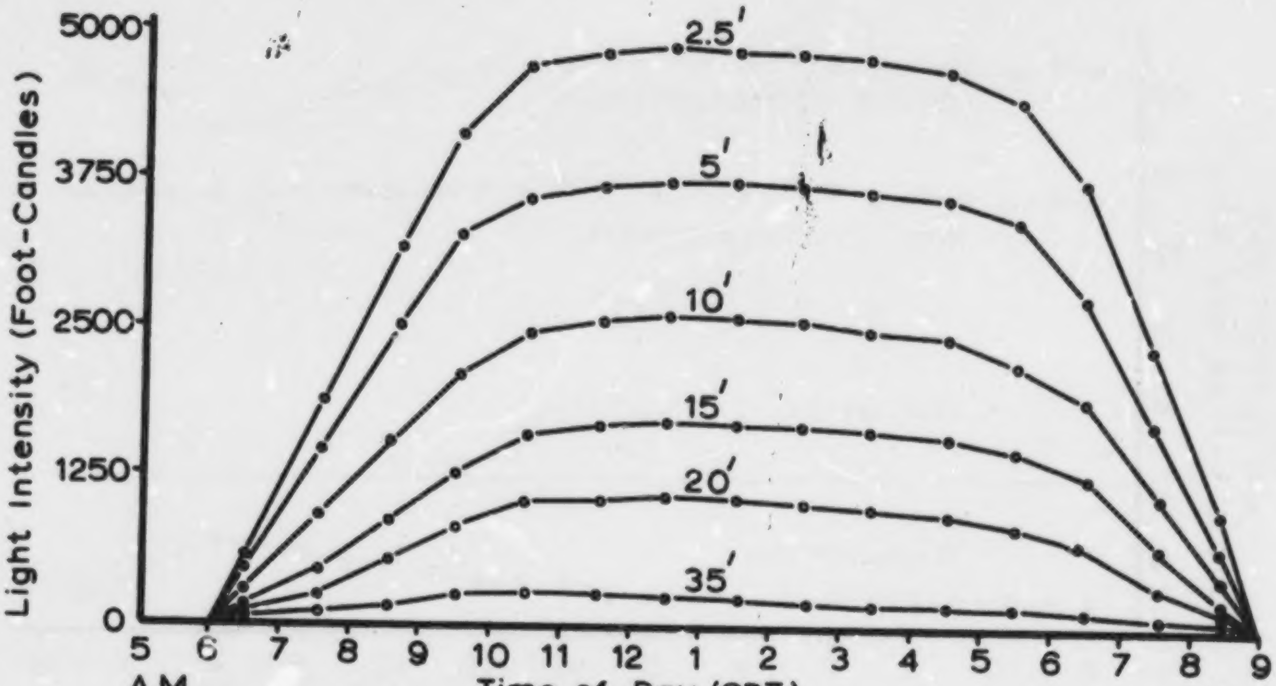

Figure 110. Calculated Hourly Light Intensity at Standard Depths in Stony Point Bay: Average for June - September, 1967.

Alteration of 1967 Photosynthesis Data

The photosynthesis data collected in 1967 under standard laboratory conditions will be useful in comparing the relative production rates of Lake Superior periphyton with those of communities in other bodies of water. If future tests on Lake Superior periphyton are run under the same standard conditions, the results can be used to detect changes in periphyton activity within the lake. However, if these data are to be viewed as a reflection of true production rates at different depths in the lake, alterations must be made to account for the effects of light intensity and temperature.

The calculated average daily variation in light intensity at each of the standard depths during the summer of 1967 is shown in Figure 110. It is obvious that photosynthesis would occur at less than the light-saturated rate for a different length of time at each station. The light intensity data from Figure 110, the temperature data from Table X, and the production rate data from Tables XXIV and XXV have been employed in the conversion of the 1967 rates to those more nearly reflecting conditions in the lake. The result of each measurement made during the first two summers could be altered according to the prevailing conditions at the time of sampling; however, to provide an example of the conversion process, only the mean photosynthetic rates for 1967 will be altered.

The mean gross photosynthetic rate of periphyton from the 2.5 foot depth in Stony Point Bay was 44.6 microliters per hour per square centimeter of rock surface (from Table XI). The respiration rate was 13.9 microliters/hour/cm^2. During thirteen daylight hours, the light intensity at the 2.5 foot depth was at the optimum level or above, so no correction is made for this factor during that period. However, the average temperature at 2.5 feet was 12.5° C. On the basis of the difference between photosynthetic rate at 20° C and 12.5° C. (interpolated), from Table XXV, the rate for those thirteen hours should be reduced by eighteen per cent, to 38.6 microliters/hour/cm^2. For two hours of daylight, both temperature and light intensity (average 600 foot-candles) were below the optimum level. The difference between photosynthetic rate at 20° C. with light saturation, and photosynthetic rate at 12.5° C. with a light intensity of 600 foot-candles, requires a reduction of the measured rate by twenty-four per cent, to 33.9 microliters/hour/cm^2. When these two figures are properly weighted, the hourly rate becomes 36.2 microliters/hour/cm^2, or 543 microliters/cm^2 for a fifteen hour day.

The average 1967 respiration rate for the 2.5 foot samples should be reduced by seven per cent to account for the apparent nighttime variation. The rate must be further reduced by eighteen per cent of the original value to account for the difference in respiration rate at 20° C. and 12.5° C. Thus the value is converted to 10.0 microliters/hour/cm^2. During a twenty-four hour day, the respiration amounts to 240 microliters/cm^2. Therefore, the resultant net photosynthetic rate becomes 303 microliters/day/cm^2, which is gross photosynthetic rate (543) minus respiration rate. This value is equal to a production rate of 1.602 grams of carbon fixed per day per square meter. The true mean production rates for the other five sampling stations were computed in a similar manner, and are presented in Table XXVI. The amount of reduction, in terms of per cent of the original value, increased considerably with increased sampling depth.

The corrected photosynthesis data and the light intensity curves can also be used to determine the efficiency of energy utilization by the periphyton of Stony Point Bay during the summer of 1967. If the energy required to form a gram-molecule of glucose is taken to be 676,000 gram-calories and is accompanied by the liberation of 22.4 x 6 liters of oxygen, then one gram-calorie will produce 190 microliters of oxygen. Since the periphyton organisms cover the substrate completely, all of the radiation within the range of 380 to 720 millimicrons reaching a particular depth is available for use in photosynthesis. The light curves in Figure 110 are based on light reception by a selenium cell, which is sensitive only to light in the photosynthetic range (Jerlov, 1966). In that range, one foot-candle is equal to 0.00398 gram-calories/hour/cm^2 (Strickland, 1958). When this conversion has been made, efficiency of energy utilization may be calculated by the use of the following equation.

$$\%\ \text{eff.} = \frac{(\text{net microliters } O_2/\text{day}/\text{cm}^2)\ (100)}{(\text{gram-calories}/\text{hour}/\text{cm}^2)\ (15)\ (190)}$$

Energy reaching the floor of Stony Point Bay during the summer of 1967 averaged 6.65 gram-calories per hour of daylight per square centimeter. Since the average net production rate was 157 microliters of oxygen produced per day per square centimeter, the efficiency of energy utilization was 0.82 per cent. This value compares favorably with the efficiency factor (1%) calculated for phytoplankton in Lake Mendota, Wisconsin, by Juday (1940). On this basis, it is concluded that periphytic algae are capable of utilizing energy as efficiently as the free-floating forms.

TABLE XXVI

PERIPHYTON PRODUCTION RATES CONVERTED TO EXPECTED RATES UNDER NATURAL CONDITIONS, STONY POINT BAY, 1967 GRAMS CARBON FIXED PER DAY PER SQUARE METER

Depth	Measured value under standard lab. conditions*	Calculated value for average lake conditions	% reduction
2.5'	1.79	1.60	10.6
5	1.30	1.12	14.0
10	0.96	0.73	16.6
15	0.63	0.50	21.2
20	0.81	0.58	28.0
35	0.57	0.17	70.2

*Standard laboratory conditions were 20°C and 1500 ft-c.

SUMMARY AND CONCLUSIONS

A comprehensive project designed to measure productivity and explore the biodynamics of Lake Superior periphyton was carried out during the summers of 1966, 1967, and 1968. The biomass, community structure, and photosynthetic activity of epilithic periphyton from a representative area, Stony Point Bay, were determined by examination of a variety of parameters. Naturally occurring periphyton and regrowth organisms were studied. In addition, the attached communities of other north shore stations were examined, although to a lesser extent. Data reflecting the effects of certain environmental conditions on the productivity of periphyton were acquired in 1968 by laboratory experimentation. These data were employed in adjusting production rates which had been determined under standard laboratory conditions during the two previous summers. Some of the more important findings and conclusions are enumerated below.

(1) Pigment concentrations show that the biomass of the periphyton of Lake Superior's north shore is similar in magnitude to other oligotrophic bodies of water. Total pigment concentrations ranged from 0.338 to 3.59 milligrams per 100 square centimeters of rock surface, and averaged 1.36 mg./100 cm^2.

(2) Pigment ratios indicate most of the north shore periphyton to be dominated by organisms of the Division Chrysophyta.

(3) Assimilation values for Stony Point Bay periphyton averaged 1.48 grams of carbon fixed per gram of chlorophyll in 1967.

(4) The total standing crop of Stony Point Bay periphyton in terms of dry weight was 55.5 tons, or 156 grams per square meter in 1967.

(5) Regrowth periphyton grew to only about one-third the biomass of naturally occurring periphyton in forty-six days. Chlorophyll levels increased by an average of 0.00057 grams per square meter per day.

(6) Net production by the periphyton in 1967 averaged 1.01 grams C fixed/M^2/day, or 3.35 grams glucose per M^2/day. The ratio of gross photosynthesis to respiration averaged 3.17.

(7) In water up to about forty feet deep in Lake Superior, periphyton can be five to six times as important in primary production as the phytoplankton.

(8) Laboratory experiments showed that alteration of light intensity (below 800 foot-candles) causes a rapid change in the chlorophyll content of the periphyton. The maximum rate of chlorophyll reduction in response to a substantial increase in light intensity was shown to be 12.7 per cent per day for eight days. The most rapid increase in chlorophyll concentration in response to a severe reduction in light intensity was 7.5 per cent per day for six days.

(9) Short-term "conditioning" of periphyton to different combinations of light intensity and temperature caused a variety of responses when photosynthetic rate was measured in crossed gradients of light intensity and temperature.

(10) Q_{10} for conditioned samples at light saturation ranged from 1.24 to 2.48. The compensation point varied from 80 to 130 foot-candles.
(11) Naturally occurring periphyton was shown to exhibit the typical "light-adapted" or "shade-adapted" photosynthetic reaction depending on the prevailing level of light intensity.
(12) The efficiency of energy utilization by Stony Point Bay periphyton was found to be 0.82 per cent, a typical value for algal communities.

It is believed that the periphyton community will be very useful in the future as an indicator of water quality, and that the data collected in the course of this investigation will provide a baseline for detecting the gradual advance of eutrophication in Lake Superior.

POSSIBLE FUTURE STUDIES

(1) What role, if any, does the periphyton play in the transfer of energy to the second trophic level? Do any animals actually feed directly on Lake Superior periphyton?

(2) What is the general level and seasonal variation of phaeophytin in naturally occurring periphyton at various depths?

(3) What are the effects of increased nutrient concentrations and increased temperature on the periphyton of Lake Superior?

(4) Is periphyton a source of phytoplankton?

(5) How much time is required for regrowth periphyton to reach the level of naturally occurring biomass?

(6) What is the level of radioactivity in the periphyton mass? The answer to this question would be of interest if a nuclear power plant were constructed on the north shore of Lake Superior.

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APPENDIX A

STATISTICAL PROCEDURES

The regression lines shown in the text were constructed using the least squares method as presented by Bancroft (1965). Procedures for determining correlation coefficients were derived from the same source. The coefficients (r) were calculated by use of the following formula:

$$r = \frac{n\sum XY - \sum X \sum Y}{\sqrt{n\sum X^2 - (\sum X)^2}\ \sqrt{n\sum Y^2 - (\sum Y)^2}}$$

In some cases, Y represents numbers of organisms and X represents chlorophyll concentration. In other correlations, Y represents photosynthetic rate, while X represents numbers of organisms. The lines were constructed to predict Y from X. The number of determinations (n) was seventeen for regular samples from 2.5, 5, 10, 15 and 20 feet. The n value for the thirty-five foot samples was sixteen. For the regrowth study, n was nine for the ten and twenty foot samples, and ten for the thirty-five foot samples. Probability values (P), which refer to the probability that r is different from zero, were determined from a correlation coefficient percentage point distribution table (Beyer, 1966).

In a general regression line, $Y = a + bX$, where a is the Y intercept and b is the slope. To determine b from the data, the following formula was used:

$$b_{yx} = \frac{n\sum XY - \sum X \sum Y}{n\sum X^2 - (\sum X)^2}$$

To determine the value of a, the calculated value of b is placed in the equation

$$Y = na + b\sum X$$

The calculated values of a and b are then inserted into the general formula $Y = a + bX$. A known value of X is inserted into the formula for the determination of the corresponding Y. The regression line is drawn through the calculated Y and the Y intercept.

APPENDIX B

SAMPLE CALCULATIONS

A. PIGMENT CONCENTRATIONS

Given:

Absorbance at 665 millimicrons = .345
645 = .122
630 = .099
510 = .111
480 = .356

Chl $\underline{a}$ (mg/L solvent) = $15.6D_{665} - 2.0D_{645} - 0.8D_{630}$;

$$\begin{array}{r}.345\\ \underline{\text{x}15.6}\\ 5.382\end{array} - \begin{array}{r}.122\\ \underline{\text{x}\ \ 2}\\ .244\end{array} - \begin{array}{r}.099\\ \underline{\text{x}\ .8}\\ .792\end{array} = \underline{4.346} \text{ mg Chl } \underline{a}\text{/L solvent}$$

Chl $\underline{b}$ (mg/L solvent) = $25.4D_{645} - 4.4D_{665} - 10.3D_{630}$;

$$\begin{array}{r}.122\\ \underline{\text{x}25.4}\\ 3.0988\end{array} - \begin{array}{r}.345\\ \underline{\text{x}\ 4.4}\\ 1.5180\end{array} - \begin{array}{r}.099\\ \underline{\text{x}10.3}\\ 1.0197\end{array} = \underline{0.5611} \text{ mg Chl } \underline{b}\text{/L solvent}$$

Chl $\underline{c}$ (MSPU/L solvent) = $109D_{630} - 12.5D_{665} - 28.7D_{645}$;

$$\begin{array}{r}.099\\ \underline{\text{x}109}\\ 10.7910\end{array} - \begin{array}{r}.345\\ \underline{\text{x}12.5}\\ 4.3125\end{array} - \begin{array}{r}.122\\ \underline{\text{x}28.7}\\ 3.5014\end{array} = \underline{2.8771} \text{ MSPU Chl } \underline{c}\text{/L solvent}$$

$D_{res},510 = D_{510} - .0026C_a - .0035C_b - .0021C_c$;

$$D_{res},510 = .1110 - \begin{array}{r}4.346\\ \underline{\text{x}.0026}\\ .0113\end{array} - \begin{array}{r}.5611\\ \underline{\text{x}.0035}\\ .0196\end{array} - \begin{array}{r}2.8771\\ \underline{\text{x}.0021}\\ .0060\end{array} = \underline{.0741}$$

$D_{res},480 = D_{480} - .0019C_a - .0136C_b - .0054C_c$;

$$D_{res},480 = .3560 - \begin{array}{r}4.346\\ \underline{\text{x}.0019}\\ .0082\end{array} - \begin{array}{r}.5611\\ \underline{\text{x}.0136}\\ .0076\end{array} - \begin{array}{r}2.8771\\ \underline{\text{x}.0054}\\ .0011\end{array} = \underline{.3391}$$

Ast. Car. (MSPU/L solvent) = $2(4.45D_{res}.510 - D_{res}.480)$

$$\begin{array}{r} .0741 \\ \underline{\mathrm{x}4.45} \\ .329 \end{array} - .3391 \mathrm{\ x\ } 2 = \underline{0} \text{ MSPU Ast. Car./L solvent}$$

Non-ast. Car. (MSPU/L solvent) =

$$7.6(D_{res}.480 - 1.49D_{res}.510)$$

$$.3391 - \begin{array}{r} .0741 \\ \underline{\mathrm{x}1.49} \\ .1034 \end{array} \mathrm{\ x\ } 7.6 = 1.7913 \text{ MSPU Non-ast. Car./L solvent}$$

$$\text{Mg (MSPU) pigment/L solvent} \mathrm{\ x\ } \frac{\text{L solvent}}{1000} \mathrm{\ x\ } \frac{\text{L sample}}{\text{L aliquot}}$$

$$\mathrm{x\ } \frac{100}{\text{cm}^2 \text{ rock surface}} = \text{Mg (MSPU) pigment/100 cm}^2 \text{ rock surface}$$

B. Q_{10} CALCULATION

Given:

Photosynthetic rate at 10°C = 12.6 microliters O_2 per mg ash-free dry weight

Photosynthetic rate at 15°C = 16.4 microliters O_2 per mg ash-free dry weight

$Q_{10} = (p_2/p_1)^{10/t_2-t_1}$

$Q_{10} = (16.4/12.6)^{10/15-10}$

$Q_{10} = (1.3)^2$

Q_{10} = 1.69 for the temperature range 10-15°